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HOMOLOGOUS GENES AND LINEAR LINKAGE IN DROSOPHILA VIRILIS

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Various species of Drosophila have produced mutations resembling in somatic appearance and in genetic behavior mutations in D. melanogaster.[1] In Sturtevant's case, involving notch in D. funebris, the resemblances to the notch of D. melanogaster are so numerous that it seems extremely probable that the two factors are similar genes in homologous loci. In the other cases, however, the similarities are not sufficient to substantiate such a conclusion.

Unfortunately, in all these instances, proof that the factors would act as allelomorphs if brought together is unavailable because the species studied do not hybridize with each other. However, even without data from hybridization, the homology of factors or of chromosomes in different species might still be detected if it were possible to demonstrate series of linked genes of which the similarly placed members have similar somatic effects. Metz has suggested that the yellow and forked genes in D. virilis are homologous with the similarly named genes in D. melanogaster. This identification, necessarily doubtful because only two factors were involved in each series, was rendered still more questionable by the discovery in D. melanogaster of singed (by Mohr) and inflated (by Weinstein[2]). The location of these factors is shown in figure 1*C*. Inflated resembles vesiculated; and if the two factors were considered homologous, it would be possible (by turning the virilis chromosome round) to homologize forked in virilis with singed in melanogaster. Singed resembles forked in its bristles, but in addition in singed flies the hairs are affected and the females are sterile. The resemblance, therefore, is not so good as that between the two forked characters; still the differences between forked in virilis and singed in melanogaster might be due to modifying factors, or the two genes might be multiple allelomorphs. While, therefore, the identification of forked and vesiculated with singed and inflated is not so

plausible as the identification of the yellow forked series in the two species, it would be impossible in the absence of further evidence to decide which interpretation, if either, is correct.

The balance of proof has swung in favor of the identification of the two yellow forked series by the discovery of the mutant crossveinless in both D. melanogaster (by Bridges) and in D. virilis (by Weinstein). In crossveinless flies of virilis (fig. 2*c*) the posterior crossvein is entirely absent, except that very rarely a small segment in the middle of the crossvein persists; the anterior crossvein is very faint and may be partly missing.

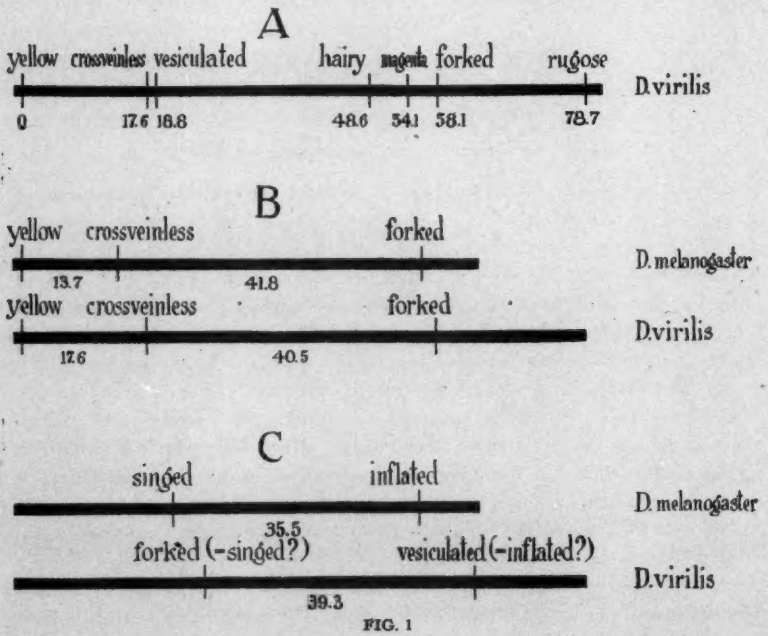

FIG. 1

In crossveinless mutants of melanogaster (fig. 2*b*), the posterior crossvein is missing, the anterior crossvein is very faint and almost entirely absent, and in addition the second longitudinal vein is slightly thickened at its distal end (see Bridges' paper elsewhere in this issue of the PROCEEDINGS, p. 660). Both factors are recessive and sex-linked, and occupy similar positions in the X chromosome with respect to yellow and forked (fig. 1*B*).

A map of the sex-linked factors of D. virilis is given in figure 1*A*.[3]

Crossveinless in Drosophila virilis.—Crossveinless in Drosophila virilis was discovered (November, 1917) in the sons of a female containing the factor yellow in one X chromosome and the factors vesiculated, hairy

magenta, and forked in the other. In the offspring of this female (number 1309, table 4*D*), which had been mated by yellow males, it was noted that all the non-vesiculated sons were crossveinless. This indicated that the locus of the new factor was in the X chromosome very near the vesiculated locus, and that the mutation had occurred in the yellow-bearing chromosome or in one of its ancestors. This chromosome had come from yellow stock, and an examination of the stock showed that a large proportion of the yellow flies were crossveinless. The success of the mutation in establishing itself in the crowded conditions of a stock bottle indicated a

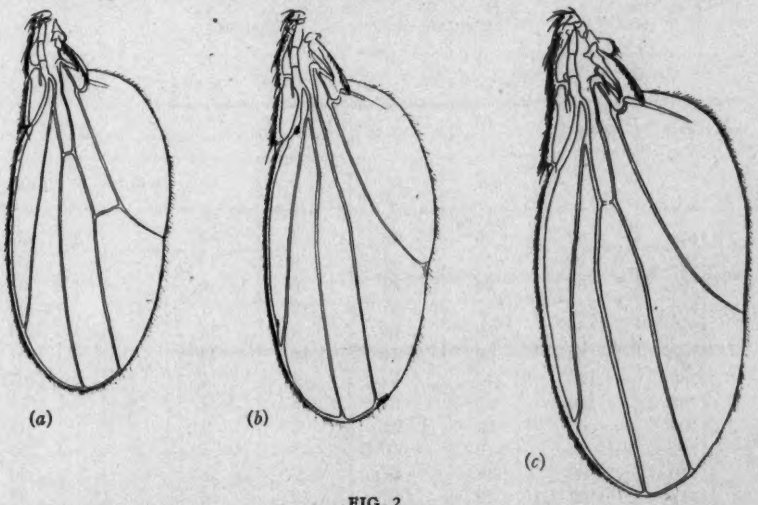

FIG. 2

(*a*) Wild-type wing of D. melanogaster (the wild-type venation of D. virilis is identical with this); (*b*) crossveinless wing of melanogaster; (*c*) crossveinless wing of virilis.

good viability, and subsequent experiments have shown that the viability is comparable to that of wild-type flies. The excellent viability and the clear-cut nature of the crossveinless character will make it very useful in determining linkage relations in D. virilis.

Crosses involving yellow, crossveinless, and vesiculated (table 1) show that the crossveinless locus lies between the other two, very near the vesiculated locus. The yellow crossveinless distance in these experiments was 19.23 units and the crossveinless vesiculated distance 1.15 units. The inclusion of other data (tables 2 and 3) lowers the yellow crossveinless distance to 17.6 units.

The determination of the crossveinless vesiculated distance may be subject to an error due to the fact that vesiculated is not a perfect diagnostic character. Vesiculated flies show the character sometimes in both wings, more often in only one, and occasionally (as we should therefore expect) in neither wing. This last point is proved by the fact that matings

of vesiculated by vesiculated sometimes produce apparently normal flies which, however, behave genetically like vesiculated. Thus an apparently normal female from vesiculated stock mated by a vesiculated male produced 35 vesiculated and 3 normal females, and 48 vesiculated and 1 normal male. It is, therefore, possible that in the present experiment some non-crossover vesiculated flies appeared normal winged and were classed as crossovers between crossveinless and vesiculated. Similarly, some flies that were genetically yellow crossveinless vesiculated may

TABLE 1

OFFSPRING OF $\frac{y\ cv}{vs}$ FEMALES*

CULTURE NO.	FEMALES	MALES						
		0		1		2		
		y cv	*vs*	*y vs*	*cv*	*y cv vs*	+	Totals
1591	62	36	29	4	4	1	3	77
1592	90	40	38	9	13		1	101
1593	69	24	29	5	5	1		64
1703	121	37	35	12	7	1		92
1704	113	59	40	9	14		1	123
1705	106	42	34	10	14		1	101
1706	120	42	43	11	9	1	1	107
1707	116	45	46	8	11		1	111
1708	52	24	21	2	1			48
1709	84	19	31	8	6	2		66
1710	88	34	43	7	6			90
1711	93	22	43	12	5			82
1712	91	38	32	11	14		1	96
1713	65	24	23	5	12		1	65
1714	59	12	18	8	1			39
1715	76	40	29	9	5	1		84
1716	88	32	23	7	6			68
1717	74	20	31	4	7			62
1718	91	31	33	7	12	1		84
Totals	1658	621	621	148	152	8	10	1560

have appeared and been classed as yellow crossveinless. This second error would tend to counterbalance the first, but only slightly, because the much larger size of the non-crossover class would make the number of vesiculated flies simulating normal much greater than the number of yellow crossveinless vesiculated flies simulating yellow crossveinless. Consequently, the crossveinless vesiculated distance, if in error, should be shorter than the calculated value. It seems, however, unlikely that in this experiment any large error was introduced in this way, because

TABLE 2

A. OFFSPRING OF $\frac{y\ cv}{m\ f}$ FEMALES

CULTURE NO.	FEMALES	MALES										
		0		1		2		3		1,2		1,3
		y cv	*m f*	*y m f*	*cv*	*y cv m f*	+	*y cv f*	*m*	*y*	*cv m f*	*y m*
1607	69	21	13	1	3	8	7					
1608	34	7	6	2		7	2		1	3		
1611	45	2	10		1	4	5		1		1	
1612	53	11	14			8	10	1				
1613	45	14	13	2	1	6	7			1	2	1
Totals...	246	55	56	5	5	33	31	1	2	4	3	1

B. OFFSPRING OF $\frac{y\ cv\ m\ f}{r}$ FEMALES.

CULTURE NO.	FEMALES	MALES																		
		0		1		2		3	4		1,2		1,3	1,4		2,4		3,4	1,2,3	1,2,4
		y cv m f	*r*	*y r*	*cv m f*	*y cv r*	*m f*	*f*	*y cv m f r*	+	*y m f*	*cv r*	*cv m r*	*y*	*cv m f r*	*y cv*	*m f r*	*y cv m*	*y m r*	*cv*
1658	110	13	14	3	7	10	16		3	8	1	3				4	1	1		
1662	69	4	9	3	1	8	5			5		1		2		2		1		
1663	110	6	21	3	2	10	9			5	1		2	2		2	1	1		1
1670	118	16	20	8	1	8	5		3	4	1	2		3		7	1		1	1
1675	57	11	13	1	4	7	3	1	1	2	2				1	6				
Totals..	464	50	77	18	15	43	38	1	7	24	5	6	2	7	1	21	3	3	1	2

C. OFFSPRING OF $\frac{y\ cv}{m\ f\ r}$ FEMALE

CULTURE NO.	FEMALES	MALES								
		0		1	2	3	4	1,4	2,3	2,4
		y cv	*m f r*	*cv*	+	*m*	*y cv r*	*cv r*	*y cv m*	*r*
1559	36	12	3	2	8	3	3	2	1	1

the complementary classes are so nearly equal. Moreover, if there was overlapping between vesiculated and normal, we should expect some genetically yellow vesiculated flies to appear merely yellow (thus simulating double crossovers); but no merely yellow flies were observed in this cross. Whatever error there may be does not influence the determination of the yellow crossveinless distance; furthermore, the order of the factors is not obscured.

Linkage of Crossveinless with Magenta and Forked.—Crosses of crossveinless with magenta and forked indicate that the crossveinless magenta distance is 36.0 and the magenta forked distance 2.7 units. This would place forked 38.7 units from crossveinless and 56.3 units from yellow. However, the crossveinless magenta distance is so long that double crossing over occurs within it (see tables 3B and 4C); and the discovery of other mutations within this region will probably move magenta and forked farther to the right. If the ratio of the crossveinless forked distances in D. virilis and D. melanogaster is the same as that of the yellow crossveinless regions (17.6 to 13.7), forked in D. virilis should be about 54 units from crossveinless and about 71 units from yellow.

The Locus of Hairy.—Crosses involving crossveinless and hairy (table 3) indicate that the two loci are about 31 units apart.

TABLE 3

A. SONS OF $\frac{y\ cv}{h}$ FEMALES

CULTURE NO.	0		1		2		1,2	
	y cv	*h*	*y h*	*cv*	*y cv h*	+	*y*	*cv h*
1563	15	13	3	2	6	9	1	
1564	6	3				4		1
1567	5	7	1	2		4		
Totals...	26	23	4	4	6	17	1	1

B. SONS OF $\frac{y\ cv\ h\ m}{}$ FEMALES

CULTURE NO.	0		1		2		3		1,2		1,3		2,3	
	y cv h m	+	*y*	*cv h m*	*y cv*	*h m*	*y cv h*	*m*	*y h m*	*cv*	*y m*	*cv h*	*y cv m*	*h*
1422	15	15	5	3	11	4			2	1		1		
1424	19	37	5	2	17	8	5	1		5	1	1	1	1
Totals.....	34	52	10	5	28	12	5	1	2	6	1	2	1	1

The second part of this table suggests that hairy lies to the left of magenta, because when these two factors separate, yellow and crossveinless generally go with hairy. This is contrary to the conclusion of Metz (1918)[1] who provisionally located hairy between magenta and forked on the basis of crosses not involving hairy and magenta simultaneously. The following crosses (table 4), in which all three factors were present at the same time, show clearly that the actual order is hairy, magenta, forked.

TABLE 4

A. OFFSPRING OF $\frac{m\ f}{h}$ FEMALES

CULTURE NO.	FEMALES	MALES					
		0		1		2	
		h	*m f*	*h m f*	+	*h f* .	*m*
1531	60	52	7		2		
1539	60	16	17	1	2	2	3
Totals.....	120	68	24	1	4	2	3

B. OFFSPRING OF $\frac{y\ m\ f}{h}$ FEMALE

CULTURE NO.	FEMALES	MALES									
		0		1		2		3	1,2	1,3	
		y m f	*h*	*y h*	*m f*	*y*	*h m f*	*y m*	+	*y h f*	*m*
1352	83	13	24	16	9	1	4	1	2	1	1

C. OFFSPRING OF $\frac{y\ \ m\ f}{vs\ h}$ FEMALES

CULTURE NO.	FEMALES	MALES											
		0		1		2		3	4	1,2		1,4	2,3
		y m f	*vs h*	*y vs h*	*m f*	*y h*	*vs m f*	*y*	*vs h f*	*y vs m f*	*h*	*m*	*vs*
1351	33	6	6	3	2	14	2	1			2		
1353	88	8	16	1	2	5		2	1	1	1	2	1
Totals...	121	14	22	4	4	19	2	3	1	1	3	2	1

TABLE 4—(*Continued*)

D. OFFSPRING OF $\frac{y}{vs\ h\ m\ f}$ FEMALE

CULTURE NO.	♀♀	MALES																							
		0		1		2		3		4		1,2		1,3		1,4		2,3		2,4		1,2,3	1,2,4		
		y	*vs h m f*	*y vs h m f*	+	*y h m f*	*vs*	*y m f*	*vs h*	*y f*	*vs h m*	*y vs*	*h m f*	*y vs h*	*m f*	*y vs h m*	*f*	*y h*	*vs m f*	*y h m*	*vs f*	*y vs m f*	*y vs f*	*h m*	
1305	102	32	4	1	3	6	10					3	1		1		1	1							
1306	59	12	1	3	4	3	6				2	2	1	1		1									
1309	104	29	14		7	11	15	2	1			2	4			1			1						
1335	147	35	9	6	9	8	16	2	3		1	9	3	1			4	1	1						1
1338	98	23	2	1	8	4	5		1	1	1						2								
1340	87	12	1		3	4	7	2									3	1							
1342	64	18	3	1	5	8	14	2		4		1													
1343	84	36	6		6	8	17	4	1	1		1	2				2				1				
1344	76	27	9	1	3	7	14			1	1	2	2				1								
1359	68	24	6	1	4	3	6		1	1			2					2		1					
1360	84	17	6	1	4	5	11	2	2	1		1		3						1					
1361	54	16	3	4	2	4	3					2	1	1						1					
1362	83	13	10	4	4	5	11		1	2	1	3					1			1			1		
1363	53	16	5	4	4	10	9	1				1			1				1			1			
Totals...	1163	310	79	27	66	86	144	15	10	11	6	27	16	6	2	2	14	5	3	4	1	1	1	1	

These results demonstrate, despite the great differential mortality in many broods, that the hairy locus is to the left of magenta; because whenever there is crossing over between hairy and magenta, forked goes with the linked gene in the magenta locus, and vesiculated (except for occasional double crossing over) goes with the linked gene in the hairy locus. If we consider only those broods in which there is no marked differential mortality (A1539 and B), we obtain the same result.

Linear Linkage in Drosophila virilis.—The data on the linkage of yellow, crossveinless, and vesiculated, and of hairy, magenta, and forked, are of interest because they demonstrate that in each case the three genes are in strictly linear order, the longest distance being the exact sum of the

TABLE 5

A. OFFSPRING OF $\frac{y}{h\ \ m}$ FEMALE

CULTURE NO.	FEMALES	MALES							
		0		1		2		1,2	TOTALS
		y	*h m*	*y h m*	+	*y m*	*h*	*m*	
1369	89	35	29	23	18	1	4	1	111

B. OFFSPRING OF $\frac{h}{m}$ FEMALE

CULTURE NO.	FEMALES	MALES			
		h	*m*	*h m*	TOTAL
1529	71	22	7	1	30

two shorter distances. Hitherto the only species for which such data have been presented has been D. melanogaster, in which, as Sturtevant, Bridges, and Morgan,[4] and Muller[5] have shown by reference to the results of critical tests, the arrangement of the genes is exactly linear. As a result of criticisms by these authors, Castle[6] has withdrawn his objections to the theory of linear linkage. In D. virilis, however, there have been hitherto no decisive data published. Metz's results, while they agree so far as they go with those in melanogaster, do not go far enough to give a decisive proof of linear arrangement. In the only case (that of hairy, magenta, and forked) in which the factors with which he worked were sufficiently close together to make a crucial test possible, he failed to make the necessary cross.

Castle, on the basis of his three dimensional theory and of Metz's data, arranged hairy, magenta, and forked, at the apices of a triangle, and predicted that the hairy magenta distance (which Metz had not determined) would be "about 4 or 5." The data now presented (tables 3 B, 4, and 5) give the hairy magenta distance as 5.5 units; or—if only those cultures are used in which the viability is good (tables 3 B; 4 A 1539, B; 5A)—the hairy magenta distance is 7.03 units.

Of course, because of the poor viability in the one case and the small numbers in the other, little reliance can be placed on these determinations as exact values. However (and this is the point at issue) the uncertainty does not affect the arrangement of the loci, which is clearly a linear one; for in all the experiments where the three loci were followed simultaneously, the frequency of separation of hairy and forked (0.1003) was the exact sum of the hairy magenta (0.0534) and the magenta forked (0.0469) separation frequencies.

Now the linear order, besides disproving Castle's triangular arrangement, shows that the values he used were not consistent with each other; for the hairy forked distance, being necessarily longer than the magenta forked distance, cannot be 3.1 if magenta forked is 3.7. The two distances, not being strictly comparable, should not be used to predict the hairy magenta distance definitely. Moreover, if the hairy magenta distance is (as Castle predicts) 4 or 5, the hairy forked distance must be longer than 4 or 5 and cannot be 3.1; that is, if Castle's predicted value is correct it follows that the value on which the prediction was based is incorrect. Thus the fulfilment of the prediction would in itself invalidate the grounds on which the prediction was based. It is therefore of no consequence whether or not the hairy magenta value recorded in this paper (5.5 for the total broods or 7.03 for those with good viability) be considered in agreement with Castle's "about 4 or 5 units"; for any agreement must be accidental and the fulfilment or non-fulfilment of Castle's prediction can have only a dramatic and not a scientific value.[7]

The loss of the hairy stock prevents any further determinations; but the data already obtained are sufficient to demonstrate that the hairy, magenta, and forked loci are arranged in strictly linear order. It has already been noted that in the cross involving simultaneously yellow, crossveinless and vesiculated, the yellow vesiculated separation frequency (20.38) is the exact sum of the yellow crossveinless (19.23) and the crossveinless vesiculated (1.15) separation frequencies. Hence, in the two only cases in D. virilis in which (because of the absence of double crossing over) the linear theory can be subjected to a decisive test, the arrangement of the genes in the chromosome turns out to be precisely linear.[8]

Castle also predicted, on the basis of his theory, that rugose and glazed would give a crossing over value of about 4 or 5 percent.; but this prediction cannot be tested directly because rugose-glazed hybrids are

sterile. It is, of course, possible to determine the crossing over value of each gene with the nearest other factor and to compare the distances thus obtained. But such an experiment is necessarily inconclusive because variations in linkage caused by other genetic factors are difficult or impossible to eliminate unless the loci to be compared are followed in the same cross.

Castle's prediction can, however, be disproved in another way, because there is evidence that rugose and glazed are allelomorphs. This is indicated by the similarity of their linkage relations (so far as tested) and of their somatic effects. Rugose dominates glazed, but this cannot be considered evidence of allelomorphism because rugose females, and hence rugose-glazed hybrid females, are wild-type in appearance. (As the factors are sex-linked there are, of course, no males carrying both together.) However, I have found that glazed females are almost invariably sterile. (Out of 146 females tested in my experiments, either singly or in mass cultures, only two produced offspring.) The sterility of glazed, while it is recessive to wild-type fertility, is dominant to the fertility of rugose, so that rugose-glazed hybrid females are sterile. This suggests strongly that the rugose and glazed genes are allelomorphic; and the evidence is strengthened by the behavior of a third mutant gene, wax, which in its somatic effects resembles rugose and glazed (though it is more extreme) and is, like them, sex-limited. Wax females, I have found, are also sterile. (Of 89 tested in my experiments, all but two failed to give offspring.) Wax eye is recessive to wild-type and to rugose, and the sterility of wax is recessive to the fertility of wild-type, but dominant to the fertility of rugose. (None of the 84 rugose-wax females tested in my experiments produced offspring.) Wax also, therefore, seems to be allelomorphic to rugose, and this is confirmed by the fact that glazed and wax behave as allelomorphs when crossed: the hybrid is intermediate and, as would be expected, sterile. (None of the 106 tested produced offspring.)[9]

Since the evidence indicates that rugose and glazed are allelomorphs, the amount of crossing over between them, if it could be directly determined, would be not about 4 or 5 per cent (as Castle predicted), but 0.

Coincidence in Drosophila virilis.—While the data in Drosophila virilis are not sufficiently extensive for any detailed considerations of coincidence, they indicate, as far as they go, that the coincidence of various regions resembles that of the corresponding regions of the X chromosome in D. melanogaster.

The values of table 6, because of the smallness of the figures and the uncertainty of vesiculated as a diagnostic character, are subject to large error; but they all agree in indicating that coincidence first

TABLE 6

COINCIDENCE IN D. VIRILIS

REGIONS	COINCIDENCE	SOURCE OF DATA
Yellow crossveinless and crossveinless vesiculated	0	This paper, table 1
Yellow crossveinless and crossveinless magenta	0.848	This paper, tables 2, 3B
Yellow vesiculated and vesiculated magenta	0.977	Metz, 1918, tables 11, 19, 22
Yellow crossveinless and magenta forked	1.4	This paper, table 2
Yellow vesiculated and magenta forked	0.989	Metz, 1918 table 19
Yellow crossveinless and forked rugose	0.795	This paper, tables 2B, C
Yellow vesiculated and forked rugose or forked glazed	0.590	Metz, 1918 tables 20, 21

increases and then decreases as the regions considered become separated farther. This agrees very closely with the conditions shown to exist in the X chromosome of D. melanogaster by Muller (1916)[10] and Weinstein (1918).[2] A similar rise and fall of coincidence have been demonstrated for the second chromosome of D. melanogaster by Bridges[2] and for the third chromosome by Gowen (1919).[11]

The Homology of Apparently Similar Factors.—Although the evidence so far obtained favors the homology of the yellow crossveinless forked series in D. virilis and D. melanogaster, it should be kept in mind that the data are by no means sufficient to make a homology certain for it is known that similar somatic effects may be produced by non-homologous genes. Thus in melanogaster there are mutant characters that resemble each other in appearance but are due to mutant genes in different loci; for example, the various eye colors resembling pink (ruby, garnet, purple, maroon, claret, etc.) and the various body colors resembling black (sable, ebony). In some cases two such "mimic" genes have been found to be very close together in the same chromosome, as in the case of miniature and dusky, which are not more than 1.8 units apart. It is obvious that a miniature mutation in virilis, even if it showed closely similar linkage relations, could not be definitely homologized with either of these two genes. A yellow virilis male with miniature wings did, indeed, occur in a cross of a yellow female by a wild-type male; and this miniature variation, if a mutation and recessive, must have been sex-linked. Unfortunately it proved sterile and its linkage relations could not be tested. Since mutations that have similar somatic effects may occur in homologous chromosomes of the same species and occupy non-homologous loci, it is certainly hazardous to take it for granted that mutations of similar effect

occurring in homologous chromosomes of different species must lie in homologous loci.

A case particularly in point in the present connection is that of the body color chlorotic, resembling yellow; its gene is close to the yellow gene in the melanogaster X chromosome. Another case is that of magenta in virilis. If forked were not known in this species, magenta might have been homologized with garnet, which is twelve units to the left of forked in melanogaster. While this identification is not entirely impossible, it is rendered rather improbable by the difference in distance from forked and by the large number of magenta-like mutants in melanogaster. The cases of singed and inflated have already been considered.

Not only may similar effects be caused by non-homologous genes, but two originally identical genes may, because of the mutation of one, or the mutation of both in different directions, or because of differences in modifying factors, come to have different somatic effects. Modifying factors may also affect the strength of linkage. The differences between crossveinless in melanogaster and virilis, and the differences between the lengths of the yellow crossveinless and the crossveinless forked distances in the two species, might be thus explained.

The order of the genes would not be affected by modifying factors (though if crossing over were entirely prevented, the order would be impossible to determine, at least in the ordinary way). But Bridges's cases of duplication and transposition[12] show that genes may be shifted to another region of the chromosome, or even to a different chromosome, without being otherwise affected; so that homologous (and indeed apparently identical) genes may come to have different linkage relations. By a combination of mutation and transposition, homologous factors might come to differ in both chemical composition and in linkage relations.

Further complications might be introduced because of duplication and of deficiency. In the vermilion duplication stock of melanogaster, each X chromosome carries two vermilion genes. Though one vermilion gene is recessive to wild-type, two vermilion genes dominate one not-vermilion. If a low cross-over factor were introduced, the two vermilion genes would remain together and would simulate the behavior of a single dominant gene. If vermilion-deficiency were substituted for one vermilion gene, the vermilion vermilion-deficiency combination would simulate a dominant vermilion with a recessive lethal effect.[13]

A similar reversal of dominance might occur because of the presence of several recessive genes in tetraploidy. Such a case could be distinguished by the frequencies of the different classes, for each factor would act as an allelomorph to each of the others.[14] Finally, there might also be reversal of dominance because of modifying factors.[15]

It must therefore be understood that while the discovery of crossveinless in D. virilis and D. melanogaster increases the probability that

the X chromosomes of the two species are composed of homologous genes, a demonstration of such homology in the absence of hybridizing experiments requires a greater number of similar genes similarly placed than have yet appeared.

Are Genes with Similar Somatic Effects Chemically Similar?—It might be supposed that factors with similar somatic effects are chemically similar even if they occupy different loci. But this supposition can be disproved by a consideration of two such factors as ruby and garnet in D. melanogaster. Each of these produces a pink eye, but the genes lie in different parts of the X chromosome. A ruby female has the composition rG/rG, a garnet female the composition Rg/Rg. Now, if $r = g$ and $R = G$, either of the above genetic compositions should produce the same effect as the composition rg/RG or rG/Rg; for in each of these cases there are two (supposedly similar) genes for pink eye color (r and g) and two (supposedly similar) allelomorphs of these (R and G). But the composition rg/RG or rG/Rg produces not a pink but a red (wild-type) eye. Hence either r differs from g, or R differ from G, or both.

This proof depends on the assumption that the position of a gene does not influence its somatic expression. The correctness of this assumption is demonstrated by Bridges'[11] cases of duplication and transposition already referred to, in which the shifting of a factor from one part of a chromosome to another or even to a different chromosome does not alter its somatic effect.

[1] Hyde, R. R., *Amer. Nat.*, **49**, 1915 (183–85, 185–187); Metz, C. W., *Genetics*, **1**, 1916 (591–607); *Ibid.*, **3**, 1918 (107–34); Sturtevant, A. H., *Science*, **48**, 1918 (72–3).

[2] Weinstein, A., *Genetics*, **3**, 1918 (135–73).

[3] D. virilis itself has been described by Sturtevant, *Ann. Ent. Soc. Amer.*, **9**, 1916 (323–43). Descriptions of the sex-linked mutants other than crossveinless will be found in Metz, *l. c.* Dscriptions of the sex-linked characters in D. melanogaster will be found in Morgan and Bridges, *Carnegie Institution Washington, Publ.*, No. 237, 1916 (1–87).

[4] Sturtevant, A. H., Bridges, C. B., Morgan, T. H., These PROCEEDINGS, **5**, 1919 (168–173); Morgan, T. H., Sturtevant, A. H., and Bridges, C. B., *Ibid.*, **6**, 1920 (162–164).

[5] Muller, H. J., *Amer. Nat.*, **54**, 1920 (97–121).

[6] Castle, W. E., These PROCEEDINGS, **5**, 1919 (25–32, 32–36); *Ibid.*, **5**, 1919 (500–506); *Ibid.*, **6**, 1920 (73–77).

[7] It was pointed out in Muller's article that the value which I had recently obtained for the hairy magenta distance was (on the data then available) 6.6, contrary to Castle's prediction; and that this, if combined according to Castle's own method with the values previously obtained by Metz in separate crosses for the hairy forked and forked magenta distances, would place the three factors in a nearly straight line in the order hairy forked magenta. This situation was used by Muller to show that, even by using Castle's method of combining separate experiments, linear results might be arrived at that were quite inconsistent with the prediction obtained by the same method. The new value, moreover, was based on more flies (total 364) than Metz's hairy forked value used by Castle (162). Muller made no claim, however, that these relationships were really correct, as it was evident that linear results arrived at by such a method

might be accidental, just as Castle's non-linear results so obtained were accidental. The fact that the order really turns out to be hairy magenta forked illustrates the latter point to a nicety and falls in line with the other results to show the fallacy of the method of combining separate experiments for a determination of the nature of linkage.

[8] It is of course possible that larger counts would give double crossovers in these cases. But this is very improbable in the case of hairy, magenta, and forked, because of the shortness of the distance involved; and even in the case of yellow, crossveinless, and vesiculated, where the distance is longer, there could scarcely be enough double crossing over to throw the factors much out of line.

[9] The sterility of rugose-glazed hybrids was first observed by Metz, who attributed it to "incompatibility," because he thought that glazed females were fertile. He had noticed their sterility when mated to rugose males, but he termed this also "incompatibility," as he believed that glazed females were not sterile when mated to glazed or to wild-type males. Now that it is known that glazed females are almost always sterile, it is obvious that the failure of the hybrids to produce offspring is due to the dominance of the sterility of glazed. In my work, each class of females (glazed, wax, and hybrids) was tested with four kinds of males (wild-type, rugose, glazed, and wax); and in all cases, with the exceptions already noted, the matings produced no offspring, though all four types of males are otherwise fertile. Metz has, consequently, withdrawn his "incompatibility" theory and accepted the interpretation given above.

[10] Muller, H. J., *Amer. Nat.*, **50**, 1916 (193–221, 284–305, 350–366, 421–434).

[11] Gowen, J. W., *Genetics*, **4**, 1919 (205–250).

[12] Bridges, C. B., *Genetics*, **2**, 1917 (445–465); *J. Gen. Physiol.*, **1**, 1919 (645–656).

[13] The yellow genes in mice and rats suggest themselves in this connection; but there is no proof that the yellow mouse case is actually like the hypothetical vermilion vermilion-deficiency combination described above, or that yellow in mice is homologous with either of the yellow factors in rats.

[14] Muller, H. J., *Amer. Nat.*, **48**, 1914 (508–512).

[15] Altenburg, E., and Muller, H. J., *Genetics*, **3**, 1920 (1–59); Bridges, C. B., and Mohr, O. L., *Genetics*, **4**, 1919 (283–306).

THE INTENSITIES OF X-RAYS OF THE L-SERIES, III. CRITICAL POTENTIALS OF THE PLATINUM AND TUNGSTEN LINES

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This work is a continuation of that of Webster and Clark[1] and Webster.[2] The methods used by them are applied to the classification of some lines that were doubtful, and the general validity of the intensity laws is tested by the use of a different metal as anticathode (tungsten).

Apparatus.—The high tension outfit constructed at the Massachusetts Institute of Technology by Prof. D. L. Webster and described in these PROCEEDINGS[3] was used without essential modification. The Chaffee

voltmeter was calibrated by measuring the current through a megohm resistance in parallel with it, and also checked by measurement of the high frequency limit of the spectrum.

The spectroscopic arrangement consisted of a large calcite crystal with a face $5^1/_2 \times 8$ cm., with a wide slit (1 cm.) placed close to the crystal and the plate about 70 cm. from the crystal. The anticathode was about 20 cm. from the crystal. With this simple setup a greater resolving power and dispersion was obtained than with the mica spectrograph used by Prof. Webster. Irregularities in the crystal gave little trouble. To exclude stray radiation the plate holder was placed in a lead box extending nearly to the crystal. In this way a considerable region of the spectrum can be mapped at once without moving the crystal; the range from 0.900 Å to 1.24 Å in the platinum spectrum, for instance, being spread over about 4 cm.

No attempt was made to measure wave-lengths directly, but for new lines the values could be found to about 0.3% by intperolation on the plate. Tubes with platinum and tungsten anticathodes and thin glass windows were kindly furnished by the General Electric Co. The former contained no iridium, but high voltage pictures showed a faint tungsten spectrum.

L-Series of Platinum and Tungsten.—The platinum and tungsten L-series, containing all lines observed with certainty here, is shown in Fig. 1. Reproductions of photographs of the region from γ_4 to β_4 are shown in Fig. 2, *a* and *b*. The tungsten spectrum has received special attention, and Dershem,[4] Overn,[5] de Broglie[6] and Siegbahn[7] have reported a large number of faint lines. All of those recorded by Siegbahn have been found, but two of the faint ones recorded by Overn only have not been observed.

In platinum, besides the 13 lines that have been followed through from element to element, we find two more lines. β_6 and γ_5, of which the wave-lengths as interpolated are 1.080 and 0.988, respectively. β_6 has been observed by Webster, while γ_5 has apparently escaped attention so far. That these two lines are really part of the platinum L-series is supported by the fact that lines occur in corresponding positions in tungsten. Thus the wave-length interval from γ_5 to γ_1, in tungsten is approximately the same as in platinum, and the same is true of the interval from β_6 to β_5.

There seems to be a real difference between the tungsten and platinum spectra as observed here. With pictures taken under similar conditions in the two elements, the relative intensity of the lines is not always the same, and some lines occur in tungsten which are apparently absent in platinum. Thus β_7, β_8, and β_9 and γ_7 which appear in tungsten are not found at all in platinum. For intensity differences, β_5 is much stronger than β_6 in platinum, but they are of about the same intensity in tungsten. There is also a change with γ_2, which is stronger than γ_3 in platinum, but

weaker than γ_3 in tungsten. In the case of both β_5 and γ_2 we are dealing with lines which lie near the absorption limits, and as there is some evidence to show a progressive shift from element to element of the absorption limits relative to β_5 and γ_2 which would bring the absorption limits on opposite sides of these two lines in platinum and tungsten, this may account for the difference in intensity here.

Another difference in intensity occurs in the case of β_4, which is stronger in platinum than it is in tungsten, but we can ascribe it to a different cause. Noticing that β_7 which is between β_1 and β_4 in tungsten is apparently absent in platinum, and that if β_4 and β_7 in tungsten were to stay at a constant wave-length interval from β_3 and β_2 respectively, they would nearly coincide in platinum, we can think of β_4 as in reality composed of these two lines. Since β_3 and β_4 belong together in L_3 and β_2 and β_7 in L_1, we would expect this wave-length interval to remain constant.

Wave-lengths of the tungsten and platinum lines in the L-series are given in table I. Siegbahn calls the line at 1.2031 β_5 but this puts it out of

TABLE I

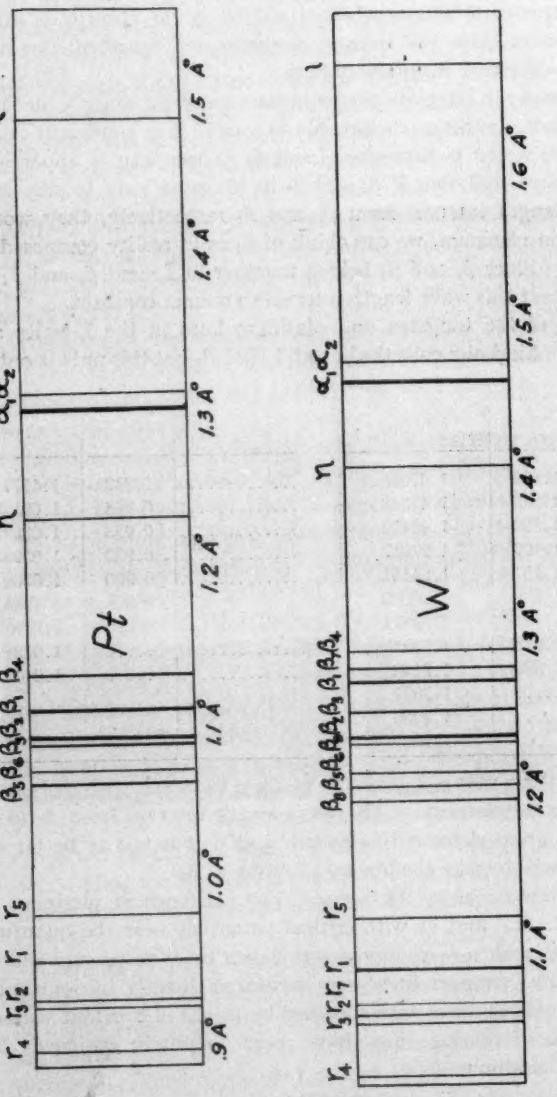
LINE	PLATINUM	TUNGSTEN	LINE	PLATINUM	TUNGSTEN
l	1.499	1.67505	η	1.242	1.4177
α_1	1.313	1.47348	γ_1	0.958	1.09553
α_2	1.323	1.48452	γ_2	0.933	1.06584
β_1	1.120	1.27917	γ_3	0.929	1.05965
β_2	1.101	1.24191	γ_4	0.900	1.02647
β_3	1.098	1.26000	γ_5	0.988	1.1284
β_4	1.142	1.29874	γ_6	.....	1.079*
β_5	1.072	1.2031	γ_7	.....	1.072
β_6	1.080	1.2118	γ_8	.....	1.044*
β_7	.....	1.2871			
β_8	.....	1.2205			
β_9	.....	1.202			

*Observed by Overn only.

line with β_5 in other elements. The wave-length interval from β_2 to β_5 is quite constant from element to element, and if it is not to be far off here, we would have to take the line at 1.2118 Å as β_5.

Assignment of the Lines to Sub-Series.—The existence in platinum of the three series L_1, L_2, and L_3 with critical potentials near the quantum potentials of β_5, γ_2 and γ_4 respectively was shown by Webster and Clark[1] and Webster.[2] The stronger lines were measured directly by ionization methods, and the weaker ones were classified by means of constant voltage photographs. The following lines have been definitely assigned, by measurements on platinum alone:

L_1 l, α_2, α_1, β_2, β_6, β_5
L_2 η, β_2, γ_1
L_3 γ_4



L-Series

FIG. 1

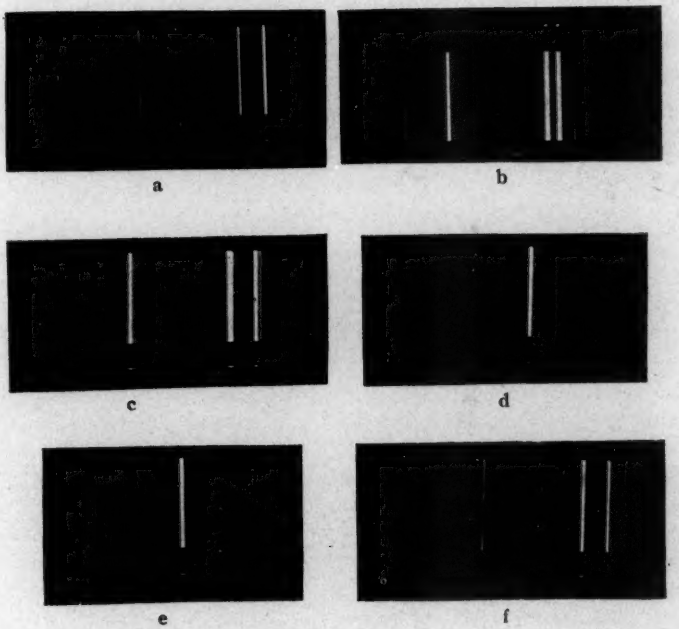


FIG. 2

In the present work these results have been confirmed. This leaves as still doubtful in platinum γ_2, γ_3, γ_5, β_4 and β_3. Of these still unclassified lines, γ_2 and γ_3 are so faint that although well resolved in all pictures, the results are still uncertain. The possibility of a fourth critical potential, as might be indicated by Sommerfeld's theory, makes these lines particularly interesting. γ_5 is too weak to show except at high voltages, with any degree of certainty. For all of these very weak lines it will be necessary to cut down the general radiation by using greater dispersion (plate farther from crystal) than is at present possible without unduly weakening the lines themselves by absorption in the air. For this purpose a vacuum spectrograph is now under construction.

β_3 is so close to β_2 in platinum as to make work on this line very difficult, but in tungsten it lies midway between β_1 and β_2. With the platinum anticathode used, where the tungsten lines also showed, the coincidence of W γ_1 with Pt β_3 was another complication, so that results were obtained on this line only in tungsten.

Pt β_4 has given rather anomalous results. Webster and Clark's[1] ionization curves showed a critical potential near V_2, but the uncertainty here was greater than with the stronger lines. In Webster's[2] photographs, however, it showed well below V_2, but the presence of a line here could be ascribed to the near coincidence of Ir β_2 with Pt β_4. With the present anticathode there were no iridium lines, and yet β_4 showed below V_2. We can account for this if we regard it as the combined line β_4 and β_7. The work with tungsten showed β_7 to be L_1 and β_4 to be L_3, so that the part showing below V_2 is simply β_7. That the ionization work indicated a critical potential the same as that of β_1 can only be ascribed to the uncertainty of the measurements on a line as weak as β_4 and to the disturbing effect of β_7, which would tend to decrease the apparent critical potential.

The results on tungsten are well illustrated by the reproductions in Fig. 2, *c*, *d*, *e*, and *f*. In *c*, *d*, and *e*, the product of current through the tube, time of exposure, and square of the voltage was made the same in all three. In *f* the time of exposure was shorter. The critical potentials calculated for tungsten would be:

V_1 10.2 kilovolts [Quantum potential of β_5]
V_2 11.6 kilovolts [Quantum potential of γ_2]
V_3 12.0 kilovolts [Quantum potential of γ_4]

These constant voltage pictures show us how β_4 and β_7 are to be classified. In *f* at 13 kv. we have them showing at nearly equal intensities. At 12.5 kv. β_4 is noticeably weaker, and at 12 kv. (V_3) β_4 is out completely, assigning it to L_3, while β_7 is still strong. At 11.5 kv., below V_2, β_7 still shows, although faint, assigning it to L_1.

That β_5 and β_6 belong together in L_1 is shown by the fact that they show with constant intensity ratio down to $11^1/_2$ kv.

β_3 disappears at 12 kv. placing it in L_3.

The evidence in these pictures would seem to put γ_2, γ_3 and γ_5 in L_3, as they show well at 12.5 kv., but are out at 12. They are still weaker, however, than β_7 which is very faint near its critical potential, so it is possible they would not show at 12 kv. even if belonging to L_2.

β_8, β_9 and γ_7 are too weak to show except at high voltages.

The behavior of the other lines that have already been classified is what would be expected. The change in intensity ratio of β_1 and β_2 is particularly noticeable. They are nearly the same at 13 kv., but quite different at 12. γ_1 behaves as would be predicted.

In some of the pictures the absorption limit of tungsten, due to absorption in the anticathode, shows near β_5, and there is also one near β_2. This latter has exactly the wave-length of Zinc $K\gamma$ and is probably due to zinc in the glass of the tube. The light spot showing in the region between γ_1 and β_5 is an imperfection in the crystal.

The classification of the lines, to date, is as given below. Those for which further work is necessary are marked with a question mark.

L_1 l, α_2, α_1, β_2, β_5, β_7

L_2 η, β_1, γ_1

L_3 β_3, β_4, $\gamma_2(?)$, $\gamma_3(?)$, $\gamma_5(?)$, γ_4

It is to be noted that the photographic method as here employed does not enable us to determine the critical potential of each line independently, as does the ionization method; but only serves to classify lines if we assume they must all fall into three series, whose critical potentials are known. It is hoped to develop a method in which quantitative intensity measurements on the plate can be made. In this way curves similar to ionization-voltage curves can be obtained.

This work has been carried out under the direct supervision of Prof. D. L. Webster, without whose very material aid it would have been impossible.

[1] Webster, D. L., and Clark, H., these PROCEEDINGS, **3**, 1917 (181–5).
[2] Webster, D. L., *Ibid.*, **6**, 1920 (26).
[3] Webster, D. L., *Ibid.*, **6**, 1920 (269–72).
[4] Dershem, E., *Physic. Rev.*, Ithaca, **11**, 1918 (461–76).
[5] Overn, O. W., *Ibid.*, **13**, 1919 (137–42).
[6] de Broglie, M., *C. R. Paris Acad. Sci.*, **169**, 1919 (962–5).
[7] Siegbahn, M., *Phil. Mag., London*, **38**, 1919 (639).

SEMINVARIANTS OF A GENERAL SYSTEM OF LINEAR HOMOGENEOUS DIFFERENTIAL EQUATIONS

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The system of linear homogeneous differential equations

$$y_i^{(m)} + \sum_{l=0}^{m-1} \sum_{k=1}^{n} \binom{m}{l} p_{ikl} y_k^{(l)} = 0, \ (i = 1,2,\ldots,n), \qquad (A)$$

where

$$y_k^{(l)} = \frac{d^l y_k}{dx^l}$$

and where p_{ikl} are functions of the independent variable x, is evidently converted into another system of the same form by the transformation

$$y_k = \sum_{\lambda=1}^{n} \alpha_{k\lambda} \bar{y}_\lambda, \qquad (k = 1,2,\ldots,n), \qquad (1)$$

where $\alpha_{k\lambda}$ are arbitrary functions of x, and where the determinant $|\alpha_{k\lambda}| = \Delta$ does not vanish identically. Furthermore, it is known[1] that (1) is the most general transformation of the dependent variables which leaves (A) unchanged in form.

A function of the coefficients of (A) and their derivatives which has the same value for (A) as for every system derived from (A) by a transformation of the form (1) is called a *seminvariant*. The seminvariants of (A) have been calculated for the case[2] $n = 1$, $m =$ any positive integer, and for the case[3] $m = 2$, $n =$ any positive integer. It is the purpose of the present paper to obtain them for the general case of (A).

The calculations are considerably simplified by first obtaining the seminvariants in a so-called semi-canonical form and then expressing them in terms of the coefficients of (A). The possibility of a simplification of this general nature was first suggested by Green.[4]

The transformation (1) converts (A) into a new system (B) in which the coefficients of the derivatives of order $m - 1$ of the dependent variables are zero provided that α_{ij} is so selected that

$$\alpha'_{ij} = -\sum_{k=1}^{n} p_{i,k,m-1}\alpha_{kj} = \sum_{k=1}^{n} q_{ik1}\alpha_{kj}, \ (i,j = 1,2,\ldots,n). \quad (2)$$

Such a selection is always possible. The system (B) is the *semicanonical* form of (A).

When the coefficients of (1) are subject to the conditions (2) it is easily proved by induction that

$$\alpha_{ij}^{(\tau)} = \sum_{k=1}^{n} q_{ik\tau}\alpha_{kj}, \tag{3}$$

where

$$q_{ik\tau} = q'_{i,k,\tau-1} + \sum_{\lambda=1}^{n} q_{i,\lambda,\tau-1}q_{\lambda k1}.$$

If π_{ikl} denotes the coefficient of (B) corresponding to p_{ikl} of (A), we find by straight substitution

$$\Delta\pi_{ikl} = \sum_{\lambda=1}^{n} A_{\lambda i}\left[\alpha_{\lambda k}^{(m-l)} + \sum_{\mu=1}^{n}\sum_{\nu=0}^{m-\lambda-l}\binom{m-l}{\nu} p_{\lambda,\mu,l+\nu}\alpha_{\mu k}^{(\nu)}\right], \quad (l = 0,1,\ldots,m-2), \tag{4}$$

where $A_{\lambda i}$ is the algebraic minor of $\alpha_{\lambda i}$ in Δ. By the use of (3) the expression (4) for π_{ikl} may be put into the form

$$\Delta\pi_{ikl} = \sum_{\lambda=1}^{n}\sum_{\mu=1}^{n} A_{\lambda i}\alpha_{\mu k}u_{\lambda\mu l}, \tag{5}$$

where

$$u_{\lambda\mu l} = q_{\lambda,\mu,m-l} - \sum_{\nu=1}^{n}\sum_{\tau=0}^{m-\lambda-l}\binom{m-l}{\tau} q_{\lambda,\nu,m-l-\tau}q_{\nu\mu\tau}.$$

Again, we find by differentiation

$$\Delta\pi'_{ikl} = \sum_{\lambda=1}^{n}\sum_{\mu=1}^{n} A_{\lambda i}\alpha_{\mu k}v_{\lambda\mu l}, \tag{6}$$

where

$$v_{\lambda\mu l} = u'_{\lambda\mu l} + \sum_{\nu=1}^{n}(q_{\nu\mu 1}u_{\lambda\nu l} - q_{\lambda\nu 1}u_{\nu\mu l}).$$

Similarly

$$\Delta\pi''_{ikl} = \sum_{\lambda=1}^{n}\sum_{\mu=1}^{n} A_{\lambda i}\alpha_{\mu k}w_{\lambda\mu l}, \tag{7}$$

where

$$w_{\lambda\mu l} = v'_{\lambda\mu l} + \sum_{\nu=1}^{n}(q_{\nu\mu 1}v_{\lambda\nu l} - q_{\lambda\nu 1}v_{\nu\mu l}).$$

From (2) it follows that the most general transformation of form (1) which leaves (B) in the semi-canonical form is given by

$$y_k = \sum_{\lambda=1}^{n} a_{k\lambda}\bar{y}_\lambda, \quad D = |a_{k\lambda}| \neq 0, \quad (k = 1,2,\ldots,n) \qquad (8)$$

where $a_{k\lambda}$ are arbitrary constants. Equation (4) shows that such a transformation converts (B) into a new system whose coefficients $\bar{\pi}_{ikl}$ and their derivatives $\bar{\pi}^{(\tau)}_{ikl}$ are given by the equations

$$D\bar{\pi}^{(\tau)}_{ikl} = \sum_{\lambda=1}^{n}\sum_{\mu=1}^{n} A_{\lambda i}\pi^{(\tau)}_{\lambda\mu l}a_{\mu k}, \qquad (l = 0,1,\ldots,m-2), \qquad (9)$$

where $A_{\lambda i}$ is the algebraic minor of $a_{\lambda i}$ in D.

If the transformation (8) is made infinitesimal, it is found that all seminvariants in their semi-canonical form must satisfy the system of partial differential equations

$$\sum_{\tau=0}^{\infty}\sum_{k=1}^{n}\left(\pi^{(\tau)}_{krl}\frac{\partial f}{\partial \pi^{(\tau)}_{ksl}} - \pi^{(\tau)}_{skl}\frac{\partial f}{\partial \pi^{(\tau)}_{rkl}}\right) = 0,$$

$$(r,s = 1,2\ldots n; l = 0,1,2\ldots,m-2). \quad (10)$$

For $\tau = 0$, $l = m-2$, there are n solutions given by[3]

$$I^{(r\,0\,0)} = \frac{1}{r!}\sum_{i=1}^{n}\left(\frac{\partial}{\partial \pi_{i,i,m-2}}\right)^r \begin{vmatrix} \pi_{1,1,m-2} & \pi_{1,2,m-2}\cdots\pi_{1,n,m-2} \\ \pi_{2,1,m-2} & \pi_{2,2,m-2}\cdots\pi_{2,n,m-2} \\ \cdots\cdots\cdots\cdots\cdots\cdots \\ \pi_{n,1,m-2} & \pi_{n,2,m-2}\cdots\pi_{n,n,m-2} \end{vmatrix}$$

$$(r = 0,1,\ldots,n-1)$$

For $\tau = 1, 2$, $l = m-2$, solutions are given by[5]

$$I^{(r\,s\,0)} = \frac{1}{s!}\sum_{i=1}^{n}\sum_{j=1}^{n}\left(\pi'_{i,j,m-2}\frac{\partial}{\partial \pi_{i,j,m-2}}\right)^s I^{(r\,0\,0)}, \ (r+s \leq n),$$

$$I^{(r\,s\,t)} = \frac{1}{t!}\sum_{i=1}^{n}\sum_{j=1}^{n}\left(\pi''_{i,j,m-2}\frac{\partial}{\partial \pi'_{i,j,m-2}}\right)^t I^{(r\,s\,0)},$$

$$(r+s \leq n; t = 1,2,3; t \leq s).$$

For $\tau = 0$, $l = 0, 1, \ldots, m-3$, n^2 solutions for each value of l are given by

$$I^{(r\,s\,t)}_l = \frac{1}{t!}\sum_{i=1}^{n}\sum_{j=1}^{n}\left(\pi_{ijl}\frac{\partial}{\partial \pi'_{i,j,m-2}}\right)^t I^{(r\,s\,0)}, \ \begin{pmatrix} r+s \leq n; t = 1,2; t \leq s; \\ l = 0,1,\ldots,m-3 \end{pmatrix}.$$

The above seminvariants may be converted into seminvariants of (A) by means of equations (5), (6), (7). A comparison of these equations with (9) shows that the desired seminvariants of (A) are obtained simply by replacing in the above semi-canonical forms π_{ikl} *by* u_{ikl}, π'_{ikl} *by* v_{ikl} and π''_{ikl} by w_{ikl}.

A comparison of the seminvariants $I^{(rst)}$ of (A) with the corresponding seminvariants[5] for the case $n = 2$ shows the former to be independent. Moreover, the functional determinant of $I_l^{(rst)}$ with respect to u_{ikl} for each value of $l = 0, 1, 2 \ldots, m-3$ shows that $I_l^{(rst)}$ are independent among themselves and of the seminvariants $I^{(rst)}$. Equations (10) show that we have the proper number of solutions for the variables involved and that all other seminvariants of the complete system can be obtained by the differentiation of $I^{(rst)}$ and $I_l^{(rst)}$. We have therefore the following theorem:

All seminvariants of (A) *are functions of* $I^{(rst)}$ $(r = 0,1 \ldots, n-1;\ r+s \leq n;\ t = 1, 2, 3;\ t \leq s)$, $I_l^{(rst)}$ $(r = 0,\ l \ldots, n-1;\ r+s \leq n;\ t = 1, 2;\ t \leq s;\ l = 0,1, \ldots m-3)$, *and of the derivatives of* $I^{(rst)}$ $(t = 1,2)$ *and* $I_l^{(rst)}$.

[1] Wilczynski, E. J., *Projective Differential Geometry of Curves and Ruled Surfaces*, Teubner, Leipzig, Chap. I.

[2] Wilczynski, E. J., *Ibid.*, Chap. II.

[3] Stouffer, E. B., *London, Proc. Math. Soc.* (Ser. 2), **15**, 1916 (217–226).

[4] Green, G. M., *Trans. Amer. Math, Soc., New York*, **16**, 1915 (1–12).

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*SOME NEW METHODS IN INTERIOR BALLISTICS**

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Read before the Academy, April 26, 1920.

The principal problem of interior ballistics is, given a particular gun, a particular shot, and a particular kind of powder, to find, for a given load, the position and velocity of the shot, the mean pressure (and incidentally temperature) of the gases in the gun, and the fraction of the powder burned, all as functions of the time or of each other until the exit of the shot from the muzzle of the gun. In particular, we wish to know the muzzle-velocity of the shot, the maximum pressure to which the gun will be exposed, and the portion of the bore which will be exposed to it. It is then the duty of the mechanical engineer to design a gun to safely resist the pressure that may be expected. Or it is the inverse problem of the ballistician, by experiments on the action of the powder in the gun, to find its properties and those of the gun. It is true that the properties of the powder are more conveniently studied by means of

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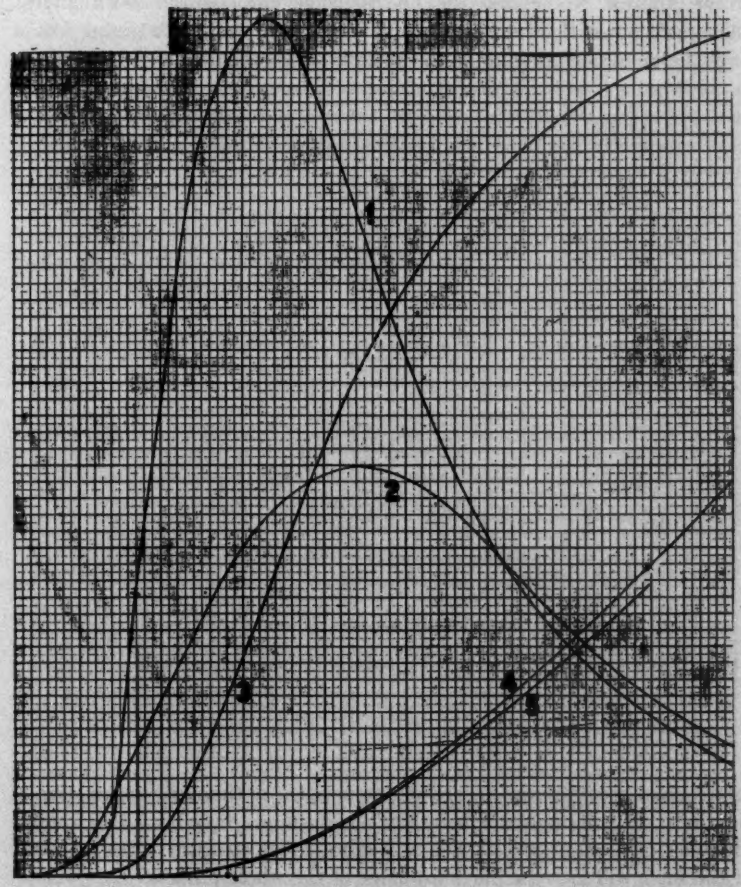
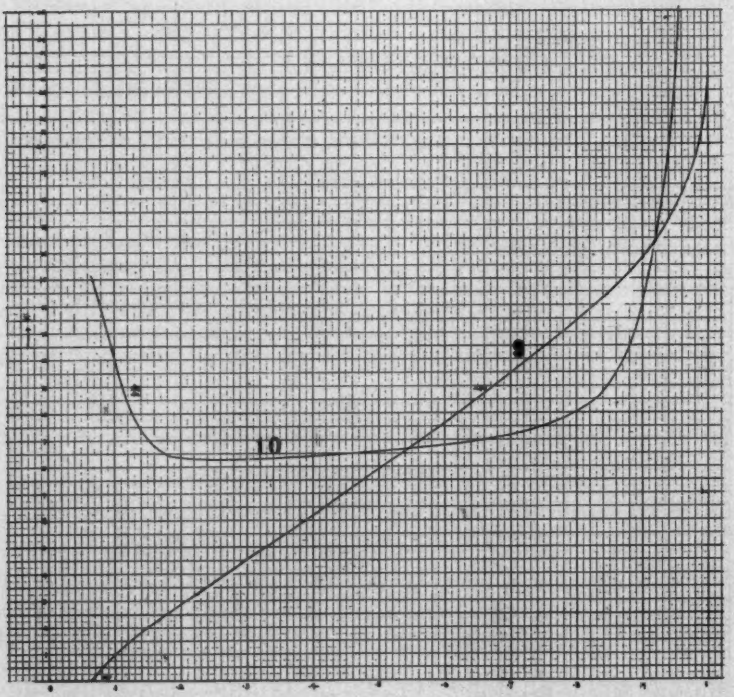
explosions in the bomb at constant volume, but we shall here show how all the properties may be determined by experiments in the gun alone.

It is customary among ballisticians to make many more or less crude hypotheses, and it is even denied that it is possible to apply the strict principles of thermodynamics to the gun as a heat-engine. It shall be our endeavor to show that this is not the case, and to relieve the subject



from some of the approximations that have usually been made. The latest and most distinguished writers upon this subject are General Charbonnier and his pupil Sugot, both members of the celebrated Commission de Gâvre (the latter its chief engineer) from which emanated all the knowledge of ballistics that was used during the war, not only for the French army but for ours.

The new methods here described consist, first, in the use of new experimental methods for obtaining the pressure in the gun, the position of the shot, and the muzzle velocity; second, in making the theory depend upon a new differential equation, and third, in the use of the graphic methods of calculation and integration that are common in engineering problems. The experimental methods hitherto have depended on the crusher gauge of Sir Andrew Noble and the Le Boulengé chronograph, both almost unchanged since their invention fifty years ago, and both giving but a single value of the pressure or the velocity. To be sure the Sébert velocimeter gives a continuous record of the position of the shot as a function of the time. It will readily be seen how a continuous record, with an infinity of values of the pressure, as well as a more direct measure of the positions of the shot, will increase our knowledge of the whole process.



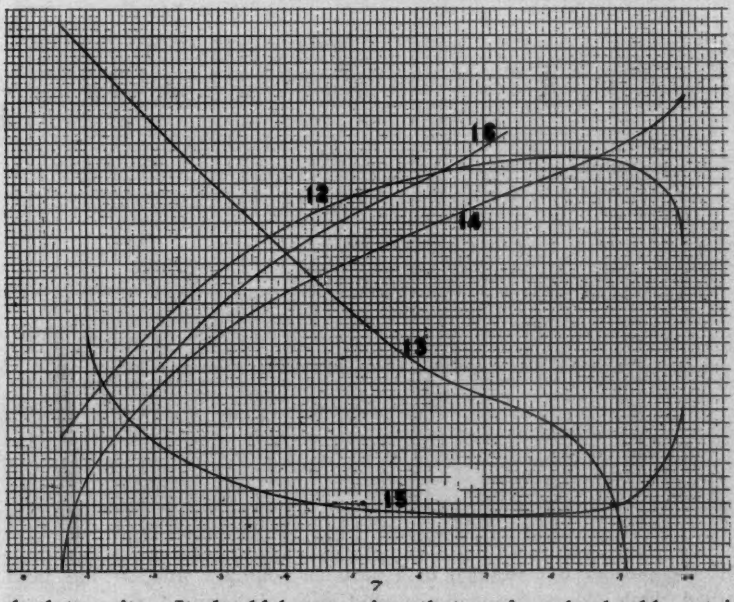
We must first decide upon the equation of state that is to be used for the gases generated by the explosion. It has been shown in a previous paper in these PROCEEDINGS (Vol. 5, pp. 286–288, July 1919) what equations of state are compatible with the constancy of the difference of specific heats at constant pressure and constant volume, and we shall use the equation of Clausius,

$$\left\{p + \frac{a}{T(v+\beta)^2}\right\}(v - \alpha) = RT, \qquad (1)$$

in the simplified form, suitable for the high temperatures concerned (2000°–3000° C)

$$p(v - \eta) = RT \qquad (2)$$

We shall use nearly the notation of Charbonnier and Sugot (*Cours de Balistique*, Imprimerie Nationale), but after having striven desperately with the multitude of engineers' units, pounds per square inch, kilograms per square centimeter or decimeter, inches or centimeters for bore and feet or meters for travel, and unknown units for velocity, acceleration and mass, we shall go back to first principle and express everything in C. G. S.

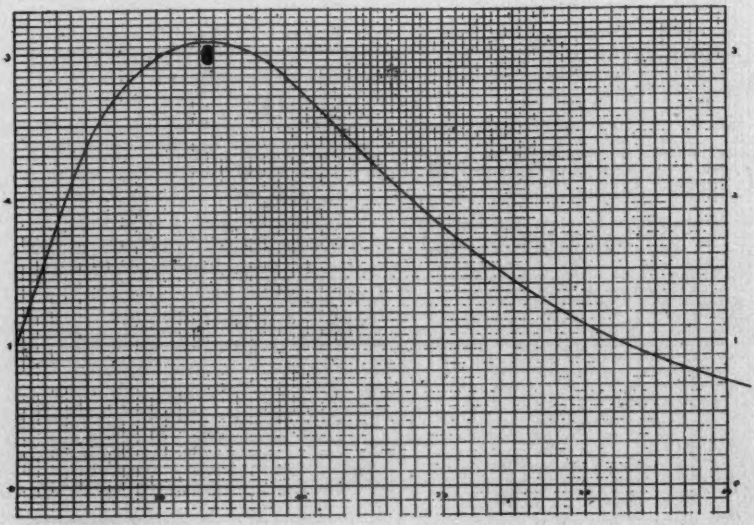


absolute units. It should be an axiom that no formula should contain any (arabic) numeral quantities except natural constants of the universe such as π, and that every formula should be correct in whatever system of units it is interpreted. It is hard to get engineers to agree to this. Consequently our unit of pressure shall be the dyne per square centimeter, with the convenience that a megadyne is between, and nearly equal to, the standard atmosphere and the kilogram per square centimeter at a place usually not specified, that v is the specific volume, in our units in cubic centimeters per gram or liters per kilogram, while T is the temperature on the absolute scale, in our units centigrade degrees. If we consider a load of powder of mass ω contained in a volume V, we define

the density of loading as $\Delta = \omega/V = 1/v$, while if the fraction of the load z has been converted into gas we have $v = V/\omega z$. Accordingly

$$p = \frac{RT}{v - \eta} = \frac{RT}{V/z - \eta} = \frac{RTz}{V - z\eta} \tag{3}$$

It is frequently assumed that during the burning the temperature of the gas remains constant, although this can hardly be the case during the expansion in the gun. Although the specific heats of the gases vary largely with the temperature, as shown by the classical experiments of Mallard and Le Chatelier (who found them to be linear functions of the temperature) we shall here consider them as constant, taking mean values. This hypothesis can be corrected later.



If the powder is contained in a variable volume c and ωz has been burned, while $\omega(1 - z)$ remains in solid form, of density δ, the gases will have the space $V = \{c - \omega(1 - z)/\delta\}$ to occupy, so that the specific volume will be $v = \{c - \frac{\omega}{\delta}(1 - z)\}/\omega z$ and we have

$$p = \frac{RT\omega z}{c - \omega(1 - z)/\delta - \omega z\eta} \tag{4}$$

as the relation between p, z, c, and T. Let S be the area of the bore, c' the volume of the chamber, and x the position or "travel" of the shot, so that

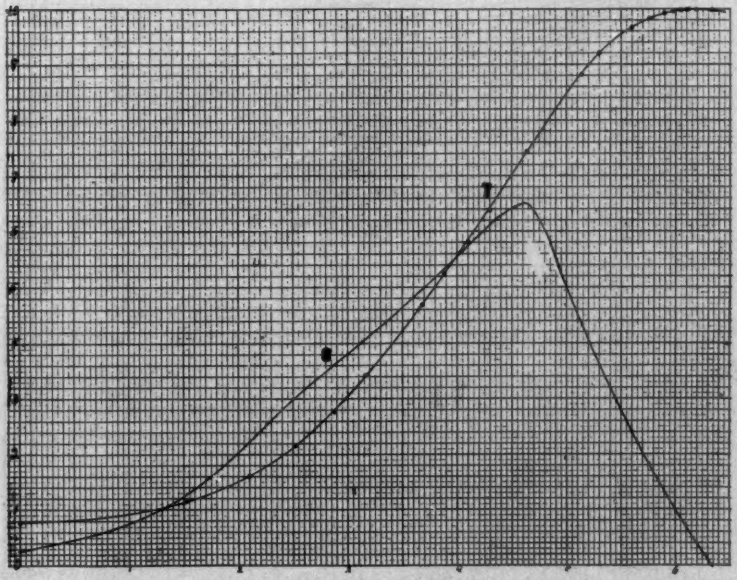
$$c = c' + Sx. \tag{5}$$

Then we have

$$p = \frac{RT\omega z}{c' + Sx - \omega(1 - z)/\delta - \omega z\eta}. \quad (6)$$

In order to write the dynamical equation of motion of the shot we shall assume that the resistance of the rifling (sometimes known as the passive resistance) which is due to the friction of the shot against the lands, and would naturally contain a term proportional to the pressure, is a linear function of the pressure

$$R = R_0 + bp. \quad (7)$$



If then m is the mass of the shot, u its velocity, t the time, and if we take account of the inertia of the gas already formed, which is really ωz, by means of a factor λ, we have

$$\frac{dx}{dt} = u, \quad (8) \qquad (m + \lambda\omega)\frac{du}{dt} = S(p - p_0) - R_0 - bp, \quad (9)$$

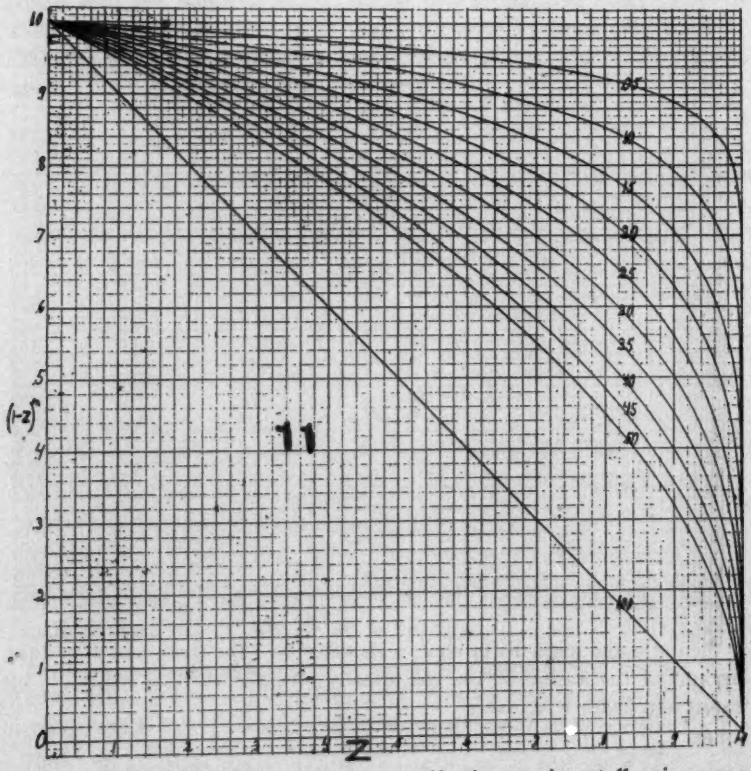
where p_0 is the atmospheric pressure, which is so small that it may generally be neglected.

By integration of (9) with respect to the time,

$$(m + \lambda\omega)u = (S - b)\int_0^t p\,dt - (Sp_0 + R_0)t, \quad (10)$$

$$(m + \lambda\omega)x = (S - b)\int_0^t dt \int_0^t p dt - (Sp_0 + R_0)t^2/2. \qquad (11)$$

If p is given in the form of a curve by the indicator, and the two integrals are evaluated for the whole time the shot is in the barrel, the determination of the muzzle velocity and of the whole length of the barrel, everything else being known, will furnish two linear equations for the determination of R_0 and b. On the other hand if the times at which the shot



passes a number of points are known, or if x is experimentally given as a function of t either of the equations (10) or (11) gives a means of verifying the assumption (7) and as many points as may be for determining the constants by least squares.

It will now be necessary to take account of the first law of thermodynamics. If U is the energy of the hot gas per unit of mass, dQ the amount of heat taken in, and Rdx the work done against friction, which is converted into heat, which stays in the gas, we have

$$dQ + Rdx = d(\omega z U) + pdV. \qquad (12)$$

If we now add (9) multiplied by (8) to (12) we have

$$dQ = (m + \lambda\omega)udu + d(\omega zU) + \frac{\omega}{\delta} pdz + Sp_o dx \qquad (13)$$

and if there are H units of heat evolved for each unit of mass of powder burned, and dq lost to the gun by conduction, we obtain the equation of conservation of energy,

$$H\omega dz - dq = (m + \lambda\omega)udu + d(\omega zU) + \frac{\omega}{\delta} pdz + Sp_o dx \quad (14)$$

Now if the specific heats are constant, we have

$$U = C_v T = \frac{RT}{\kappa - 1} = \frac{p(v - \eta)}{\kappa - 1} \qquad (15)$$

where κ is the ratio of the specific heats. The quantity of heat $Hdz - pdz/\delta$ may be determined by calorimetric experiments in a bomb at constant volume, as is seen by putting dx and du equal to zero. Putting this equal to $fdz/(\kappa - 1)$ as is customary, neglecting q and p_o, which can be done, and integrating (14) we have

$$\frac{f\omega z}{\kappa - 1} = (m + \lambda\omega)\frac{u^2}{2} + \frac{\omega zRT}{\kappa - 1} \qquad (16)$$

which is Résal's equation, given in 1864. Combining this with (6) we eliminate the unknown temperature, which has never been experimentally determined, and obtain

$$p = \frac{f\omega z - \frac{1}{2}(\kappa - 1)(m + \lambda\omega)u^2.}{c' + Sx - \omega(1 - z)/\delta - \omega\eta z} \qquad (17)$$

From this, if p, x, and u are experimentally determined, we may calculate z for each position of the shot.

If we could neglect u^2, or if it were proportional to z and if x, p, z, were taken as coördinates, this would be the equation of an hyperbolic paraboloid, of which the sections $z = const.$ are called *isopyric* lines by Lieut. Col. Hadcock in his paper on Internal Ballistics (*Proceedings Royal Society*, July 1, 1918 (479–509)). Col. Hadcock states that the expansion is neither adiabatic nor isothermal, but something between the two. This is true enough, as will be shown later, but it can hardly be justifiable to put, with any value of ϵ, Col. Hadcock's equation (5) $p(v - \alpha)^\epsilon/z^\epsilon = K$, for this makes the pressure proportional to z^ϵ, instead of a linear fractional function of z. The assumption that u^2/z is constant is not exactly true, but might be adopted without great error, as we shall see.

If we now put for brevity,

$$\frac{c'}{\omega} - \frac{1}{\delta} = B, \frac{S}{\omega} = C, \eta - \frac{1}{\delta} = D, \frac{S-b}{m+\lambda\omega} = E, \qquad (18)$$

$$\frac{R_0 + Sp_0}{S-b} = F, \left(\frac{m}{\omega} + \lambda\right)\left(\frac{\kappa - 1}{2}\right) = G$$

where B and C are constants depending on the load, D a constant of the powder, E a constant of the gun and shot, and G a mixed mass and specific heat constant, or $g = f - Gu^2/z$ an approximate constant, we may write

$$p = \frac{fz - Gx^2}{B + Cx - Dz} \qquad (19)$$

$$p = \frac{gz}{B + Cx - Dz} \qquad (20)$$

We have heretofore said nothing about the rate of burning of the powder. After the powder is all consumed, $z = 1$, and the expansion is adiabatic. We are interested in the period of combustion. It is now customary to assume, after Charbonnier, that the rapidity of burning of the powder is a function of the amount already burned, the function $\varphi(z)$ being known as the form function of combustion, while a factor A is called the vivacity, being, for a given powder, inversely proportional to the linear dimensions of the grain of given form. The rate of burning is also proportional to some increasing function of the presssure, let us say $P(p)$. The simplest functions, except linear functions, are some powers of the variables, not in this case integral powers. If the power is progressive we take $\varphi(z) = z^\beta$, if degressive (as in our powders), $\varphi(z) = (1 - z)^\beta$. We will also put $P = p^\alpha$, where α is positive, as the burning is faster the greater the pressure. We accordingly put

$$\frac{dz}{dt} = A\varphi(z)P(p) = A(1 - z)^\beta p^\alpha. \qquad (21)$$

We thus have the three simultaneous equations,

$$dt = \frac{dz}{A\varphi(z)P(p)} = \frac{dx}{u} = \frac{du}{E(p - F)}. \qquad (22)$$

It is obvious that the simplest choice for independent variable is z, accordingly we take

$$\frac{dx}{dz} = \frac{u}{A\varphi(z)P(p)}, \qquad (23) \qquad \frac{du}{dz} = \frac{E\,(p - F)}{A\varphi(z)P(p)}, \qquad (24)$$

and eliminating u by differentiation,

$$\frac{d^2x}{dz^2} = \frac{1}{A\varphi P}\frac{du}{dz} - \frac{u}{A\varphi^2P^2}\left(P\varphi' + \varphi P'\frac{dp}{dx}\right) = \frac{E(p-F)}{A^2\varphi^2P^2} - \frac{dx}{dz}\left(\frac{P'}{P}\frac{dp}{dz} + \frac{\varphi'}{\varphi}\right). \quad (25)$$

Now by logarithmic differentiation of (19) we obtain

$$\frac{1}{p}\frac{dp}{dz} = \frac{f - 2Gu\frac{du}{dz}}{fz - Gu^2} - \frac{C\frac{dx}{dz} - D}{B + Cx - Dz} \quad (26)$$

or by means of (23), (24)

$$\frac{dp}{dz} = p\left\{\frac{f - 2GE(p-F)\frac{dx}{dz}}{fz - GA^2\varphi^2P^2\left(\frac{dx}{dz}\right)^2} - \frac{C\frac{dx}{dz} - D}{B + Cx - Dz}\right\}, \quad (27)$$

so that we have finally

$$\frac{d^2x}{dz^2} = \frac{E(p-F)}{A^2\varphi^2P^2} - \frac{dx}{dz}\left[\frac{\varphi'}{\varphi} + p\frac{P'}{P}\left\{\frac{f - 2GE(p-E)\frac{dx}{dz}}{fz - GA^2\varphi^2P^2\left(\frac{dx}{dz}\right)^2} - \frac{C\frac{dx}{dz} - D}{B + Cx - Dz}\right\}\right] \quad (28)$$

This is a sufficiently complicated equation of the second order and of the third degree in dx/dz, but it is exact, and no simplifying assumptions have been made. If we know φ, P, p being obtained from equation (19), it gives x, the travel of the shot, in terms of z, the fraction of the powder burned. The equation (28) may be integrated graphically. When x is known as a function of z, p may be so determined, and then t and u from equations (22). Thus x, p, u, and z may all be found in terms of t, and the direct problem is solved. The equation (28) will be considerably simplified if we neglect G, which is equivalent to assuming the temperature constant, which is usually done.

We shall however use the differential equation (28) or rather (25) to solve the inverse problem. If x, p, and u are experimentally given, from which z is calculated by (19), everything in (28) is known except P and φ. If we begin with an approximate value of φ, say $(1-z)^\beta$ and an assumed value of p^α, equation (28) will be a linear equation for α and β, from which by a few trials, the exact values may be obtained.

We now come to the experimental portion of the work. The pressures in the rifle were observed by means of the gauge described in these PROCEEDINGS for July, 1919, the film being afterwards placed in the lantern and an enlarged tracing being made with a pencil on squared paper. From

this the calculations were made by my assistant, Dr. E. A. Harrington, who has carried out all the experimental work except the determination of the travel of the shot. In the figures (p. 649), curve 1 represents p,t for the shot used, while 2 is a curve of a reduced charge of 7/10 normal. The curves were then graphically integrated twice by counting the squares. Curves 3 and 4 show the first and second integrals $\int pdt$ and $\int dt \int pdt$, respectively. The travel of the shot was determined by observing the time of contact of the bullet with the end of a coil of fine wire forced down the barrel to a measured point, an oscillograph of high frequency being used, and the time being observed on one of the revolving drums previously described. This was done about a year ago by my then assistant, Mr. H. C. Parker, and the result, shown in curve 5, is the average of a good many shots. The exact agreement of the two curves 4, 5 shows the propriety of the assumption about the resistance, and determines b as $(S-b)/S = 0.894$. In this case $R_0 = 0$. We can also neglect p_0 so that $F = 0$.

The muzzle velocity and the time of the shot leaving the barrel were determined by the method described in these PROCEEDINGS, April, 1920, developed in this laboratory by Thompson, Hickman, and Riffolt. The constants of the gun were as follows:

Volume of chamber, $c = 4.18$ cm.
Area of bore, $S = .456$ cm.

As for the constants of the powder, the density was determined by Dr. Harrington in the pyknometer as 1.58 gm./cm. No attempt was made to determine η experimentally, that being best done in the bomb, but the value $\eta = 0.95$ was assumed. The load was $\omega = 3.100$ gm. To determine f, the "force" of the powder (which has the dimensions of energy/mass) two methods were used, which agreed very well. If it is assumed that the point of inflexion on the observed pressure curve marks the end of combustion, $z = 1$, f is determined from equation (19). If, on the other hand, equation (19) is used with observed values of p, x, and u, it will give values of z increasing to a maximum, and then diminishing. This maximum should be equal to unity, and after a few trials a value of f can be found that makes it so. As stated, this method agrees with the other. We obtain $f = 1.087 \times 10^{10}$ cm.^{2}/sec.^{2}, corresponding very well with the values for the French powders and cordite. (The values given by Charbonnier and Sugot involve gravitation units.) We thus obtain

$B = 0.716$ cm.^{3}/gm., $C = 0.147$ cm.^{2}/gm.,
$D = 0.32$ cm.^{3}/gm., $E = 0.394$ cm.^{2}/gm.

If we take $\kappa = 1.2$, and $\lambda = 0.2$, we have $G = 0.333$. Also we find that g (eq. 20) varies by about 16%, nearly as a linear function of x or z.

In order to show the functional relation (19) between the five quantities p, x, u, z, G, an "*abaque à glissement*" was constructed, so that by placing a transparent index on four of the variables the fifth could be found. This will be described elsewhere, but inasmuch as it was found to take longer to set the index than to set up the numbers on the arithmometer, of which we have several models, it was not used. After z was calculated, curves were drawn: $6(p,x)$, the indicator diagram (p. 652) for the gun; $7(z,t)$, $8(dz/dt,t)$, $9(x,z)$, $10(dx/dz,z)$, $11(1-z)^n$ for various values of n; $12(p,z)$, $13(dp/dz,z)$ (with a different zero of ordinates); $14(u,z)$; $15(du/dz,z)$; $16(dz/dt,z)$.

For graphical differentiation, a simple contrivance was used consisting of two metal rulers jointed together at one end. Near the other end of one was placed a plane mirror normal to the edge of the rule. By looking at the curve in this, and making its reflection join it without a corner, the direction of tangency could be found more accurately than by making the ruler tangent. The other ruler is then set parallel to the horizontal lines of the paper, and for a horizontal distance of ten or twenty centimeters the vertical distance between the rules read off, giving the trigonometrical tangent. Thus in a few minutes we may lay down the derivative curve with nearly three figure accuracy.

I have the following criticisms to make on the curves. After they had been given to the photographer it was discovered that the left-hand portions of (9) and (10) are incorrect, since dx/dz must vanish when x and u are zero. This is probably due to an error in choosing this point, which should be at the inflexion of the p curve, which should have been determined with the mirror directly on the film, instead of on the enlargement. When this is done, the pressure to start the shot is found to be the same as on curve 2, which (like 1) is so good that films of two different shots may be laid one over the other without being distinguishable. Making this correction will slightly displace curves (3) and (4). I realize that I have given hardly enough here to verify the theory, but as this paper is too long already, and as I am very shorthanded for assistance, I consider it best to publish it for the method, and to leave the verification, which should be by the construction of the observed curves from calculation, for another paper. By the courtesy of Rear-Admiral Ralph Earle, we have a Naval one-pounder gun, to which we hope to apply the methods, on which we hope to improve by experience. For a larger gun, where the wires might be blown out of the gun by the blast, we have another method of finding the velocity in the bore.

It should have been stated in our former paper, and is now stated here, that these experiments have been made possible by means of a generous grant from the Rumford Fund of the American Academy of Arts and Sciences, and to my colleagues on the Rumford Committee I hereby express my hearty thanks.

THE MUTANT CROSSVEINLESS IN DROSOPHILA MELANOGASTER*

BY CALVIN B. BRIDGES

DEPARTMENT OF ZOÖLOGY, COLUMBIA UNIVERSITY

Communicated by T. H. Morgan, September 30, 1920

The Origin of Crossveinless.—A recessive sex-linked mutant called small-eye appeared, the locus of which was found to be very close to that of fused (locus of *fu*, 59.5). To determine definitely the relation of the two loci, a forked (locus of *f*, 56.5) small-eye (symbol, *sy*) female was crossed to a fused male, and five of the F_1 wild-type females were mated singly to forked small-eye brothers. In F_2, no crossovers between small-eye and fused were obtained. While this result confirms the closeness of the loci, it was decided to raise more F_2 cultures until one or more cross-overs appeared which would show the position of the new locus with reference to the known loci forked and fused. Accordingly, from one of the five F_2 cultures (No. 10,846) four wild-type females, of the same constitution as the original F_1 female, were mated to forked small-eye brothers. There appeared two cross-overs (wild-type) that showed that the locus of small-eye is to the left of that of fused (and about 0.2 unit distant, i.e., at 59.3).

In one of these four cultures it was noticed (No. 10,988, Dec. 21, 1919) that about half the males did not have either anterior or posterior cross-veins. All females had normal crossveins. Evidently crossveinless (*cv*) is a sex-linked recessive. The other three sister cultures were then examined, and no crossveinless flies were present.

The males that hatched after the mutant character was noticed were: *cv f sy* 12, *fu* 11, *cv fu* 3, *f sy* 9. Since approximately half the males showed the crossveinless character, the mother is known to have been heterozygous for the mutant gene. The crossveinless character emerged in association with forked more often than with fused, which means that the mutant gene was in the forked small-eye chromosome of the mother. She had received this chromosome from her father—the F_1 forked small-eye male used in raising culture 10,846. But three of her sisters likewise received forked small-eye sperm from this same male, and, as we have seen, none of these three sisters received the crossveinless gene. It follows that the mutation occurred relatively late in the ontogeny of the testis of the male in question, perhaps as late as the maturation stage.

The Locus of Crossveinless.—Of the thirty-five males in which the linkage relations of crossveinless to forked, small-eye, and fused were noted, 12, or 34.3%, were crossovers between crossveinless and forked. In view of the small numbers, this value indicated only that the locus of crossveinless is to the left of that of forked and probably at least as

* Contribution from the Carnegie Institution of Washington.

distant as vermilion (*v* locus, 33.0). The next step was to mate a crossveinless forked small-eye male to a vermilion female and to raise several F_2 cultures (table 1).

TABLE 1

P_1, CROSSVEINLESS FORKED SMALL-EYE ♂ × VERMILION ♀; F_1 WILD-TYPE ♀, $\frac{cv \quad f \quad sy}{v}$ × F_1 VERMILION ♂ (TABLE INCLUDES F_2 ♂ ♂ ONLY)

JAN. 20, 1920	0		1		2		3		1,2		1,3	
	cv f sy	*v*	*cv v*	*f sy*	*cv*	*v f sy*	*cv f*	*v sy*	*cv v f sy*	+	*cy v sy*	*f*
11223	64	60	19	15	22	17	3	1	1	1	–	–
11225	41	63	16	19	18	10	1	–	1	2	–	–
11226	42	52	16	14	25	14	2	2	1	2	1	–
11227	63	62	18	10	19	16	1	–	–	2	1	–
11268	102	84	29	24	39	31	1	1	4	4	–	–
11275	89	110	31	27	27	33	1	3	2	3	–	–
11276	10	22	3	4	5	8	–	1	–	2	–	1
Total.....	411	453	132	113	155	129	9	8	9	16	2	1

The locus of crossveinless, on the basis of the F_2 males, proved to be about 19.0 units to the left of vermilion, that is, about 14 units from the zero end of the chromosome. This location is regarded as especially valuable since the interval from ruby (7.5) to cut (20.0) did not contain any serviceable mutant character. The rather poor mutants club (16.7), lemon (17.5), shifted (17.8), and depressed (18.0) had all been lost or discarded. It was important to have a mutant of first rank in this region in order to investigate the linkage behavior of lethal-2, which is probably a "deficiency." A multiple stock, ruby cut tan (*t*, 27.5) vermilion had been made up for this analysis, and it was decided to incorporate the crossveinless character in the multiple. In the process of incorporating crossveinless, accurate knowledge of the location of crossveinless was obtained from the F_2 results of the cross between crossveinless male and females of the original multiple (table 2).

There was 8.5% of crossing over between ruby and crossveinless, and 8.3% between crossveinless and cut. The locus of crossveinless is thus almost exactly in the middle of the gap between ruby and cut. The total amount of crossing over between ruby and cut was 16.8 which is slightly higher than the expected value 12.5.

This position of crossveinless makes it possible to study linkage relations in any part of, or throughout the *X*-chromosome, by means of mutants so close together than no unobserved double crossing over occurs. Furthermore, these mutants are perfectly classifiable in combination, and, with the exception of cleft at the extreme right end of the chromo-

TABLE 2

P_1, CROSSVEINLESS ♂ × RUBY CUT TAN VERMILION ♀; F_1 WILD-TYPE ♀, $\frac{rb \quad ct\ t\ v}{cv}$, × F_1 *rb ct t v* ♂ (TABLE INCLUDES F_2 ♂ ♂ ONLY)

	0		1		2		3		4		1,3		1,4		2,3	2,4
FEB. 14, 1920	*rb ct t v*	*cv*	*rb cv*	*ct t v*	*rb*	*cv ct t v*	*rb ct*	*cv t v*	*rb ct t*	*cv v*	*rb cv t v*	*ct*	*rb cv v*	*ct t*	*rb t v*	*rb v*
11328	63	87	6	15	17	14	10	7	7	7	–	1	–	–	–	–
11329	62	74	12	6	8	7	7	5	8	5	1	2	3	1	1	1
11330	75	77	6	5	7	4	10	9	6	6	–	–	–	–	–	1
11331	86	74	15	4	8	5	9	9	7	7	–	–	–	–	–	–
11332	72	87	5	8	6	12	10	6	2	17	1	–	–	–	–	–
11333	75	77	10	8	10	7	10	6	10	6	1	–	–	–	–	–
11400	47	44	4	8	4	4	5	2	5	5	–	–	–	–	–	–
11418	59	70	10	5	9	8	5	8	3	2	–	–	1	–	1	–
Total.....	539	590	68	59	69	61	66	52	48	55	3	3	4	1	2	2

some, are of such excellent viability that they can be used simultaneously with only negligible differential mortality. Crossveinless is one of the best of these characters, since the somatic effect is so slight that interference with the classification of other mutants is at a minimum. It is a matter of observation that mutants like crossveinless with slight somatic effects are generally those with least disturbance to viability. A striking example of this correlation is to be found in the cut mutations. On at least eleven occasions sex-linked mutations that were similar to the original cut have appeared. Of these, cut[3] was both the poorest in viability and the most extreme in extent and number of somatic changes, while cut[6] was the best in viability and least extreme in its single observed somatic change. Two of the other allelomorphs, were intermediates in

TABLE 3

P_1, CROSSVEINLESS ♀ × CUT[6] ♂; F_1 WILD-TYPE ♀, $\frac{cv}{ct^6}$, × F_1 *cv* ♂ (F_2 ♂ ♂ ONLY)

APR. 14, '20	*cv*	*ct*[6]	*cv ct*[6]	+	CONT.	*cv*	*ct*[6]	*cv ct*[6]	+
11700	88	95	9	8	11733	228	235	15	14
11701	81	75	7	7	11734	143	164	11	12
11702	108	106	7	10	11735	89	88	6	7
11703	22	26	2	2	11736	135	156	7	12
11704	91	88	4	5					
					Total.....	985	1033	68	77

both these regards, while differing from each other. Cut[6] is now the only cut mutant used for linkage determinations involving this locus.

Additional linkage data upon the crossveinless cut distance was obtained by raising nine F_2 cultures from the cross of crossveinless to cut[6]. The crossover value was found to be 6.7 on the basis of the 2,163 flies (table 3).

The locus of crossveinless is at 13.7, as calculated on the basis of the data of the three preceeding tables, and on the assumptions that the locus of ruby is at 7.5 of cut at 20.0, and of vermilion at 33.0.

Description of the Crossveinless Character; Homology with Crossveinless in D. virilis.—The somatic changes produced by the crossveinless gene seem to be restricted to the entire absence of the posterior crossvein and the almost complete absence of the anterior crossvein. There is a slight trace only of the anterior crossvein, though on casual inspection it seems to extend outward from the III-longitudinal vein about half way to the IV[th]. However, what is seen is largely a sense-organ that is normally present near the mid-point of the anterior crossvein and that is not affected by the crossveinless mutation. Examination of crossveinless in D. virilis showed that the sense organ is unaffected there also, but that the crossvein is not reduced in length or thickness as much as in D. melanogaster. (See figures of the crossveinless mutant in Weinstein's paper preceding this.)

The similarity of the characters is parallelled by a similarity of position on the maps of the two *X*-chromosomes. It seems highly probable that the two mutants are homologous, though, as Weinstein's discussion brings out, this cannot yet be accepted without reservations.

IS CROSSING OVER A FUNCTION OF DISTANCE?[1]

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Communicated by C. B. Davenport, September 24, 1920

There is a well intrenched concept of recent genetics that hereditary factors or genes may be given fairly definite loci on chromosome maps and that these maps correspond to or represent, roughly perhaps, the actual conditions in the chromosome. The basis for this attractive and suggestive view is the premise that the distance between two genes is necessarily proportional to the percentage of crossing over which these two genes show—other things being equal. If the distance which gives one per cent of crossovers is used as an arbitrary unit of measurement, then it follows that distances on the chromosome may be calculated in terms of this unit. It has seemed to me for some time that the antecedent in this hypothetical proposition contains a more or less gratuitous assumption.

We do not know that the distance which gives 1% (or n%) of crossovers is a fixed unit. Stated differently, we do not know how constant the percentage of crossing over may be between two genes to which we give a fixed distance, i. e., our arbitrary unit of measurement may itself prove to be a variable. It may be possible for the distance which gives 1% of crossing over to differ in different females of the same population, or differ between stocks. In order to throw some light on these questions I began a set of experiemnts in 1916 in collaboration with my colleague, Dr. E. Roberts, and several students. Although a number of these experiments are still in progress, data involving the classification of over 400,000 individuals have been accumulated and some conclusions seem warranted. A more detailed account of these experiments will appear in the current numbers of the *Journal of Experimental Zoölogy*.

In observing a large number of females (Drosophila melanogaster) of the generalized zygotic formula $\frac{a\ b}{A\ B}$, it is common to find great differences between individual females with respect to the amount of crossing over. Some of the variability may be due to sheer fluctuations of sampling, to age, and to environmental conditions, but sometimes the deviations are so wide as to arouse a suspicion that hitherto unknown causes may be effective. If this variability is due at least in part to genetic modifiers then selection should be effective, particularly if environmental fluctuations do not mask or obliterate the effects of genetic modifiers. It was with this thought in mind that I began to select for high and low crossover value. Four selection experiments were undertaken. Series A, A' and B were low selection experiments and Series C was a high selection experiment. Each series began with a single white-eyed, miniature-winged female mated to a wild, red, long male. The F_1 females were red, long double heterogzyotes $\frac{w\ m}{W\ M}$ and the F_1 males were white, miniature double recessives $\underline{w\ m}$. These were mated in pairs, giving the parental classes (red long and white miniature) and the crossovers (red miniature and white long) with the usual ratio of approximately 33% crossovers—the same value used in plotting chromosome maps. The same mating was made in successive generations, always selecting as far as was possible the widest deviates to perpetuate the line of selection. At the same time, the closest possible inbreeding was maintained, the details of which are given in our longer papers. The results indicate that selection was effective in all series.

Series A was reduced to 0% in F_{10} and remained at about 0% for two more generations. Series A', derived from Series A as a side line of selection in the F_7, began with a female showing 1 : 91 = 1.10%.[2] This line was carried for 9 generations (F_7–F_{15}) and also bred true to about 0%. The grand total for this *entire series* gave 33 : 5156 = 0.64%—actually

less than 1 %. There can be no doubt but that an original crossover value of about 33% has been changed by selection, at least a marked change has followed selection.

Series *B* was entirely independent in its origin from Series *A* and *A'*; and low selection was also effective, as in the case of the preceding series. Curiously enough we have not been able as yet to reduce the crossover value to zero, or approximately zero, as in the other series. Since experiments with this series form the basis of the present paper, table 1 is given to show in condensed form the progress during selection. After the F_{28}, selection was discontinued, and the stock has bred practically true to about 5 or 6% crossing over for 22 generations (i. e., through F_{50}). Table 1 gives the percentage of crossovers for every fifth generation, and also for the total offspring in each block of five successive generations.

TABLE 1

CROSSOVER VALUES FOR EVERY FIFTH GENERATION, AND FOR THE TOTALS IN EACH BLOCK OF FIVE SUCCESSIVE GENERATIONS, IN SERIES *B* (LOW SELECTION)

GENERATIONS	CROSSOVER VALUES	GENERATIONS INCLUDED	CROSSOVERS	TOTALS	CROSSOVER VALUES
1	28.60	1– 5	10517	40567	25.93
5	24.55	6–10	10344	47295	21.87
10	16.99	11–15	3687	25333	14.55
15	11.17	16–20	4869	48277	10.09
20	9.81	21–25	3386	36693	9.23
25	7.15	26–30	576	8007	7.19
30	5.62	31–35	121	2089	6.79
35	4.18	36–40	267	4571	5.84
40	6.70	41–45	750	12453	6.02
45	6.51	46–50	350	5203	6.73
50	6.98				

Series *C*, high selection, was carried for 8 generations, but we were unable to make progress in selecting upward. On the contrary, we were greatly astonished to find in the F_7, 9 out of 72 pairs, which gave almost no crossing over at all, although they produced a large number of offspring. The remaining 63 pairs gave about the usual crossover value. The totals for these 9 paired matings were:

26 crossovers : 1055 total = 2.46% crossing over.

These same genes should have given 33% crossing over if they agreed with the usual values used in plotting chromosome maps. The natural inference is that any attempt to increase crossing over leads to double crossing over and thus to very low crossover values (practically zero). The explanation implies that these 9 females showed a marked *decrease* in crossover values, despite high selection, because they gave almost nothing but double crossovers. Series *C* was dropped, but we hope to

repeat the experiment and test out the region between white and miniature in such females.

The effects of selection on crossover values may be due to one or a number of causes, some of which suggest themselves almost immediately. The most promising and probable explanation seemed to me to be that crossing over is either due to or markedly modified by multiple factors. In order to test out this view, I crossed the low crossover stock of Series *B*, which shows 5–6% crossing over, to ordinary stock which shows 33% crossing over. Table 2 gives the results of this experiment. The first line of the table gives for comparison the frequency distribution of crossover values in an ordinary population. There were 90 females in this sample but I have eliminated two very wide deviates from the distribution, because the number of offspring on which their crossover values were based was extremely small. One of them showed 1 : 8 = 12.5%; and the other showed 6 : 8 = 75%. The population as a whole showed 30.68% crossing over and the mean female had a value of 30.55%. The average number of offspring per female and the totals show that the values for the females both individually and collectively are as reliable as can be reasonably expected. The second line of the table shows the first generation in Series *B*, which resembles closely the sample just described. After 28 generations, selection was discontinued. Thereafter the generations were perpetuated by en masse matings. In the F_{42}, I mated 50 red, long females heterozygous in white miniature $\frac{w\ m}{W\ M}$ to stock white miniature males $\underline{w\ m}$. All except one were fertile and the distribution of their crossover values is given as the low P_1 parent in table 2. Mating them to ordinary stock males would not change the crossover values which such low females show. We cannot know positively what the crossover value of each white miniature male parent was, but we have no reason to suppose it differs greatly from the values given for the first generation of Series *B* or the ordinary stock, both shown in table 2. We have used this same white miniature stock in class work and have always found it to give the regular "map value" of about 33%.

It was virtually impossible to breed all of the F_1 hybrid females from each pair separately. I decided to breed exhaustively 50 red long F_1 females $\frac{w\ m}{W\ M}$ to their F_1 white miniature brothers $\underline{w\ m}$ to obtain a sample frequency distribution of F_1 females coming from a single P_1 pair (pair No. 18). Forty-seven of these 50 females were fertile and gave an average of 465 offspring per female.[3] The range of F_1 crossover values shows quite clearly that they lie between the low and the high parents. The value of the mean female and the crossover value of this total F_1 population show the same thing. One F_1 female showed a ratio of 1 : 36 = 2.77%, but since the ratio is based upon such a small total we need not lay much stress on this wide variate.

TABLE 2

THE DISTRIBUTION OF CROSSOVER VALUES IN NORMAL POPULATION, IN LOW CROSSOVER STOCK, AND IN HYBRIDS BETWEEN THESE

GENERATIONS	NUMBER OF VARIATES	THE DISTRIBUTION OF CROSSOVER VALUES															MEAN VARIATE	σ	CROSS-OVERS	TOTAL	% OF CROSS-OVERS	AVERAGE NUMBER OF PROGENY PER VARIATE
		1.5	4.5	7.5	10.5	13.5	16.5	19.5	22.5	25.5	28.5	31.5	34.5	37.5	40.5							
Sample population	88								7	11	19	28	15	5	3		30.55	4.28	6465	21071	30.68	239.4
1st generation, Series *B*	34							3	5	3	10	6	3	2	2		28.85	5.58	2056	7189	28.60	211.4
P_1 low patent	49	7	26	15	1												5.11	2.10	425	7948	5.35	162.2
F_1 hybrid females	47	1		2	10	16	12	6									13.88	3.64	3216	21853	14.72	465.0
F_1 samples of each P_1	45			10	18	10	6	1									11.50	3.10	5213	39416	13.23	875.9
F_2 from P_1 No. 2	33	2	1	5	8	8	5	3	1								12.24	4.90	1060	7812	13.57	236.7
F_2 from P_1 No. 5	39				5	13	12	5	1	2			1				16.19	4.70	1477	9001	16.41	230.8
F_2 from P_1 No. 6	76		1	3	14	23	22	6	3	3	1						14.96	4.39	3161	21701	14.57	285.5
F_2 total	148	2	2	8	27	44	39	14	5	5	1		1				14.66	4.81	5698	38514	14.79	260.2

In addition to the F_1 distribution coming from a single P_1 pair, I also obtained a sample crossover value of the F_1 coming from each of 44 other P_1 females. I chose at random four F_1 red, long double heterozygotes from each P_1 pair. Each group of four F_1 females was mated to white miniature F_1 brothers. Thus we secured crossover values for 45 different F_1 groups, each group coming from a single P_1 pair. These F_1 crossover values are put in the form of a frequency distribution in the fifth row of table 2. Here again we find the F_1 values intermediate between the low stock and the original population. In no case was an F_1 value as low as the mean or mode of the low parent nor as high as the mean or mode of the original population.

Three distinct and separate F_2 distributions were reared, coming from P_1 pairs No. 2, 5 and 6. The value of each original P_1 female, together with the crossover ratio of its F_1 and F_2 progeny, is given in table 3.

TABLE 3

THE DATA ON P_1 PAIRS NO. 2, 5, AND 6, FROM WHICH THE F_2 DISTRIBUTIONS WERE OBTAINED

P_1 PAIR NO.	CROSSOVER VALUE	F_1 CROSSOVER VALUE	F_2 CROSSOVER VALUE
2	21:382 = 5.50	29: 464 = 6.25	1060: 7812 = 13.57
5	7:193 = 3.63	72: 530 = 13.59	1477: 9001 = 16.41
6	6:178 = 3.37	251:1730 = 14.51	3161:21701 = 14.57

The F_2 distributions of table 2 show a wider range than the low parent or the F_1. In fact, the total F_2 population with 148 pairs gives some females as low as the low parent and some as high as the original population. The mode is between the two stocks. It is clear that the results of these hybridization experiments bear the distinctive features of multiple factor inheritance with incomplete dominance; for the F_1 is intermediate and the F_2 is likewise intermediate in its average but the F_2 shows a conspicuous increase in range which easily overlaps both original P_1 distributions. The increase in the standard deviation of each F_2 population and of the total F_2 distribution over that of the F_1 or P_1 puts these facts in concrete terms. Therefore, we can hardly escape the conclusion that multiple factors have a striking influence upon crossover values. In the frequency distributions of table 2, some variates will necessarily have little meaning because their crossover values are based upon small totals. I have thought it desirable to include every variate and thus withhold no data rather than include only such females as produced more than a fixed minimum of offspring. However, in order to show that the extremes in the F_2 population are segregates, rather than fluctuations of sampling, I have given in table 4, detailed data on the highest and lowest 12 variates in the total F_2 frequency distribution of table 2. The lowest 12 variates have values from 0%–9% and cover about the same range as the low

parent; while the highest 12 have values above 21% and cover about the same range as the high parent. The values for both low and high F_2 variates are based upon totals which are just as satisfactory as any in the population, where the average number of progeny per female was 260. The total F_1 included 61,000 offspring and the total F_2 distribution is based upon 38,500 offspring.

TABLE 4

THE HIGH AND LOW VARIATES OF THE TOTAL F_2 DISTRIBUTION IN TABLE 2

LOW VARIATES					HIGH VARIATES				
RECORD NUMBER	CROSS-OVERS	:	TOTAL =	CROSSOVER VALUE	RECORD NUMBER	CROSS-OVERS	:	TOTAL =	CROSSOVER VALUE
2– 2	1	:	35 =	2.86	2–32	66	:	287 =	23.00
2– 6	18	:	216 =	8.33	5–21	52	:	154 =	33.77
2–19	14	:	223 =	6.28	5–22	45	:	178 =	25.28
2–22	0	:	19 =	0.00	5–24	69	:	325 =	21.23
2–25	8	:	168 =	4.76	5–28	112	:	466 =	24.03
2–28	14	:	174 =	8.05	6–10	107	:	416 =	25.72
2–33	22	:	329 =	6.69	6–21	56	:	241 =	23.24
2–34	25	:	280 =	8.93	6–23	71	:	287 =	24.74
6– 8	11	:	281 =	3.91	6–24	61	:	251 =	24.30
6– 1*a*	32	:	394 =	8.12	6–11*a*	33	:	145 =	22.76
6– 2*a*	23	:	275 =	8.36	6–13*a*	26	:	89 =	29.21
6–35*a*	20	:	272 =	7.35	6–16*a*	62	:	295 =	21.02
Total.....	188	:	2666 =	7.05	Total.....	760	:	3134 =	24.25

In obtaining a crossover value for any two genes like white and miniature we find much variability among the females which serve to make up the general population from which our map value is derived. This variability is due to numerous modifying factors. Selection has evidently sifted out certain relatively pure combinations of these modifiers, hence the low variability of our low crossover stock. The hybridization experiments indicate that the amount of crossing over is at least markedly influenced if indeed it is not actually determined by multiple factors. There are several ways in which multiple factors might possibly change the crossover value which two genes show. In modifying the crossover value of white and miniature from 33% to 6% or to 0% we might suppose that we had either moved the locus of genes or that we had eliminated the usual single chromosomal twist between these two genes. Since the allelomorphic relationships between red and white and between long and miniature have not been disturbed when we mate low crossover stock to the original population, the latter alternative explanation seems preferable. We can evidently change by selection the amount of twisting which members of an homologous pair of chromosomes show. Now, if the difference between practically no crossing over (Series A and A') or between 6% crossing over (Series B) and normal crossing over (33%) is due to multiple

factors, we then naturally wonder just what part "distance between two genes" on a chromosome map may play in determining linkage values. Our current view is that "the percentage of cases in which two linked genes separate (amount of crossing over between them) is necessarily proportional to the distance between these genes,—other things being equal," i. e., under ordinary circumstances and in the absence of unusual factors or environmental conditions which geneticists recognize. But evidently under ordinary circumstances, the percentage of crossing over is a variable which is determined by the different possible combinations of multiple modifying factors; hence the percentage of crossing over cannot be proportional to the distance if the distance remain constant. For example in Series *B* we find 6% crossing over, and so we should conclude that the distance is less than one-fifth of what it originally was before we began selection. To maintain our original position, we must conclude that the percentage of crossing over and the distance are correlated variables, if the proportion is to remain reasonably constant. The dilemma will hardly aid us in determining what had happened to almost all of the distance and the genes between 0 and 33 in Series *A* and *A'*, where crossing over was practically eliminated. In view of these considerations it would perhaps be simpler to conclude that linkage is not a function of distance, i. e., crossing over is not necessarily proportional to distance. The distance between two genes may remain fairly constant, but the amount of crossing over depends upon numerous hereditary factors.

[1] Paper No. 14 from the Laboratory of Genetics, Illinois Agricultural Experiment Station.

[2] In giving crossover values, I shall put the data in the following form throughout this paper—crossovers: total = per cent of crossing over. Since the classes are always the same, repetition can be avoided.

[3] I am indebted to Dr. E. Roberts and Mr. P. M. Woodworth for carrying this generation in part.

INTERSPECIFIC HYBRIDS IN CREPIS

I. *Crepis capillaris* (L) Wallr. × *C. tectorum* L.

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Interspecific hybrids, particularly those having different specific chromosome numbers, have in the past figured conspicuously in establishing the now generally accepted principle of the individuality and continuity of the chromosomes. It is probable, therefore, that a study of the hereditary characters of species hybrids may give further information concerning the chromosomes as the carriers of the determiners of hereditary characters

and add to our knowledge regarding the manner of the origin and evolution of specific chromosome numbers.

From a study of interspecific crosses between *Nicotiana sylvestris* and several varieties of *Nicotiana Tabacum*, Clausen and Goodspeed[1] have found that the Mendelian laws apply but apparently the chromosomes of the hybrid will function normally only when there is a union of a majority of the chromosomes of one species. When the chromosomes of one gamete are mostly of a different species from those of the other uniting gamete the zygote either does not live or it develops abnormally. This seems to indicate that although they are numerically the same, the chromosomes of the two species differ so much qualitatively that they cannot properly function together.

Eggs of the sea urchin have been fertilized artificially with the sperm of another species in which the chromosomes were different in number. In practically all such cases the zygote would start but fail to complete development. It appears that the chromosome complex sets up an incompatible combination of genes such that the embryo cannot pass a certain stage of differentiation.

The writers have found a somewhat similar case in plants in the hybrid between *Crepis capillaris* and *C. tectorum*. This genus belongs to that tribe of the Compositae having the heads composed entirely of ligulate flowers. *C. tectorum* is an annual and *C. capillaris* behaves either as an annual or as a biennial. The former has four pairs of chromosomes while the latter, *C. capillaris*, has but three pairs. Cytological studies have shown the hybrid to have seven chromosomes, the sum of the haploid numbers of the two species.

The differences between the two species are quite marked. The achenes of *tectorum* are about 4 mm. long, are dark brown in color and retain the pappus quite well. The cotyledons are narrowly linear with obtuse apex, the shape resembling that of a sunflower seed or the cotyledons of a very young cucumber seedling. The first plumule leaf appears very promptly soon after the cotyledons have expanded and reached their maximum size. The plants often reach maturity in ninety days. The achenes of *capillaris* are about 2.5 mm. long, are tan or straw color, and shed the pappus rather easily. The cotyledons vary from broadly ovate to the condition where the breadth is slightly greater than the length. As in *tectorum* the first plumule leaf appears very promptly after the cotyledons have expanded to their normal size.

In the hybrid, regardless of the way the cross is made, we find that the *tectorum* type of cotyledon is dominant but the seedlings are larger than the normal *tectorum* seedlings and may in that respect be said to show hybrid vigor. That the shape and size of the hybrid cotyledons growing on a *tectorum* mother plant would be comparable to the cotyledons

from a pure *tectorum* achene of the same size would not be surprising but that the cotyledons coming from the much smaller *capillaris* achenes should be so much larger than those usually coming from ordinary *capillaris* achenes seems unusual and gives immediate evidence of the hybrid nature of the seedling.

The hybrid seedlings grew very vigorously through the cotyledon stage, then growth and development ceased although different plants remained alive from 30 to 81 days in this arrested condition. All hybrids died before passing beyond this stage of development. The attempt to grow the hybrid between these two species was made three separate times always with the same behavior and the same results.

TABULATION OF RESULTS OF RECIPROCAL CROSSES

CULTURE NO.	PARENTS	COTYLEDON CHARACTERS OF HYBRID	BEHAVIOR OF HYBRID	NUMBER OF SEEDLINGS
Z 3	*capillaris* × *tectorum*	6 *tectorum*, 5 *capillaris*, 1 intermediate	all failed to pass cotyledon stage	12
Z 5	*capillaris* × *tectorum*	all *tectorum;* showed hybrid vigor	all failed to pass cotyledon stage	6
Z 7	*capillaris* × *tectorum*	all *tectorum;* showed hybrid vigor	all failed to pass cotyledon stage	3
Z 8	*capillaris* × *tectorum*	intermediate	failed to pass cotyledon stage	1
Z 10	*tectorum* × *capillaris*	all *tectorum;* showed hybrid vigor	all failed to pass cotyledon stage	12
Z 12	*capillaris* × *tectorum*	small and distorted, abnormal	failed to pass cotyledon stage	1
Z 13	*capillaris* × *tectorum*	small and distorted, abnormal	all failed to pass cotyledon stage	5

Histological examination of a hybrid seedling revealed a most unusual teratological condition of the tissue systems and of the cells which, no doubt, was the immediate cause of the unusual behavior noted. These tissue systems were in a chaotic condition where order and continuity should be expected. Patches of embryonic tissue were scattered irregularly among the vegetative cells, patches of tracheary cells were likewise found here and there in the meristematic tissue of the seedling. In fact, tracheary cells were in one section found to be extending at right angles to the long axis of the seedling. Groups of vegetative cells were separated by streaks of disorganized and disintegrating tissue. Some of the vegetative cells were abnormally large.

In this interspecific hybrid it appears as if the force directing cell differ-

entiation were lacking or non-functioning. We know that in all promeristematic cells there must be the potentiality for development of a complete individual but that during development something determines what, when and where tissues and organs shall be developed. In these hybrids that force is not acting, in a normal way at least, and hence the cells develop the various tissues in a haphazard way and otherwise misbehave.

The opinion has been expressed a number of times that the different species of a single genus having different chromosome numbers may have been derived, the larger from the smaller number, by fragmentation or by duplication resulting from non-disjunction during synopsis. Rosenberg[2] has recently worked out the specific chromosome number of 15 species of Crepis (published 19, 4 having been determined by other cytologists). He expressed the belief that the species having four and five pairs of chromosomes could have been formed by non-disjunction occurring during the reduction division. Bridges[3] has shown that such behavior is possible, at least for the sex chromosomes in Drosophila, for he has found flies with ten chromosomes, the typical number for the species being eight. The increased number came about through secondary non-disjunction of the sex chromosomes in both parents. This fly, a female, was able to live and reproduce. These two cases are not, however, equivalent since the ten-chromosome Drosophila had the regular female content plus two Y chromosomes which are not known to influence the production of characters except that absence of the Y chromosome causes sterility of the males.

Whether a zygote containing a duplicated pair of chromosomes can go through development may depend entirely upon which pair is duplicated. From our knowledge of the chromosome numerical variations in Oenothera and Primula certainly it is possible for a plant to develop to maturity with one extra chromosome or with an entire duplicate set.

The behavior of the seven-chromosome Crepis hybrid leads us to believe that there is not such a direct relationship between the two parent species as Rosenberg suggests. However, this in no way does violence to Rosenberg's hypothesis, for *C. tectorum* may behave in quite a different way when crossed with some other three paired chromosome species of Crepis.

It is possible that more light may soon be thrown upon this side of the problem inasmuch as there are now 36 species of Crepis with which trial crosses are being made to further test their chromosome relationships.

[1] Clausen, R. E., and Goodspeed, T. H., *Proc. Nat. Acad. Sci.*, **2**, 1916 (240–44).
[2] Rosenberg, O., *Arkiv. för Botanik.*, **15**, 1918 (11).
[3] Bridges, C. B., *Genetics*, **1**, 1, 1916 (1–52; 107–63).

NEW OBSERVATIONS ON THE VARIABILITY OF THE SUN

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Read before the Academy, April 26, 1920

Photometric Observations of the Planets.—(*a*) Simultaneous spectrobolometric observations of the solar constant of radiation in California and Algeria in 1911 and 1912, and in California and Chile in 1918, (*b*) comparisons of the distribution of radiation over the sun's disk with simultaneous measurements of the intensity of total solar radiation, (*c*) comparisons of the temperature of the earth with the radiation of the sun, and (*d*) several other minor evidences, have all indicated a short irregular periodicity in the sun's emission. In other words, the sun appears to be a variable star ranging through about 0.10 stellar magnitude between extremes and often changing 0.03 magnitude within a few days.

If this is so it must follow that the planets are also variable because they reflect solar light. Guthnick and Prager have made accurate photoelectric photometric comparisons of Saturn and Jupiter with available stars. Their published results led them to state a conclusion adverse to the solar variability (*Veröffentlichungen K. Sternwarte Berlin-Babelsberg*, **2**, Heft III, 1918 (126)). I wrote to Dr. Guthnick pointing out that this conclusion was premature, because the number of published photometric observations was not large, and they might have fallen on dates when the sun's emission was nearly the same. No direct solar observations were available on those dates. Dr. Guthnick has kindly reopened his investigation and sent me results for January, February, March, April and May, 1920.

We have available for comparison on almost all these days observations of the sun by Smithsonian observers at Calama, Chile. But it is not obvious that a comparison between the brightness of the planets and that of the sun should involve identical dates. Two hypotheses of solar variation may be made. First, the sun's emission may vary in all directions proportionally and simultaneously. Second, the sun may be surrounded by a ragged absorbing or radiating envelope so that his emission is unequal in different directions. Under this second hypothesis the rotation of the sun would carry with it shafts of unequal radiation, which would encounter the planets successively according to their heliocentric longitudes. This second hypothesis is plausible in view of the dissymmetry of the solar corona. It has the advantage, too, of not requiring rapid changes of the sun's emission, which would be hard to account for in view of the immensity of the sun.

Dr. Guthnick states that Jupiter varied irregularly and widely in surface conditions during the period of observation so that its fluctuations are not available for solar constant comparisons. Various well-known

causes of variation in addition to the supposed solar changes affect the brightness of Saturn. In the observations recently sent to me Dr. Guthnick has corrected for all of these influences except those associated with phase. These produce quite a large effect, so that, for instance, the comparisons between Saturn and α Leonis show gradually progressive differences ranging from 0.61 to 0.90 stellar magnitude. He states that for 1920 observations the influence of phase is approximately eliminated by subtracting from the given magnitude differences the product of the phase angle in degrees by a coefficient, which before opposition is 0.025, but after opposition is 0.039. These correcting coefficients are, however, inapplicable for observations made within less than 1° of opposition. Saturn then becomes considerably brighter than would be expected.

I have reduced the observations on Saturn to constant phase angle by applying the coefficients just mentioned. On three dates, namely, Feb. 25, Feb. 28 and March 1, the phase angle is less than 0.5°, so that the corrections are not applicable for these dates. The observation of March 13 is stated by Dr. Guthnick to be of small weight because of unfavorable sky conditions in Berlin. Those of April 23 and May 12 are not of very great weight because Saturn was too near the horizon.

In a first comparison I employed solar constant observations made in Chile on even dates with the observations made in Berlin. The result was so unsatisfactory as in my judgment to discredit the first hypothesis of a solar variation, appearing simultaneously in all directions. I then turned to the second hypothesis, making allowance for differences of heliocentric longitude of the earth and Saturn, and also for differences of terrestrial longitude and times of observing between Chile and Berlin. I thus arrived at the results given in the following table. In addition to the six days mentioned above as unsuitable, Feb. 7 is also unsatisfactory, owing to very cloudy conditions in Chile.

There remain nine days suitable for comparison. These nine days are on the whole favorable to the view that the sun and Saturn each varied in brightness by two per cent, and that their variations were synchronous and proportional. The largest discrepancy which occurs among these nine comparisons is for March 9.5/10 and it indicates an error of slightly more than 0.5 per cent, or 0.005 magnitude. This amount of error is surely to be expected occasionally. Indeed it is very remarkable how accurate the results appear to be both in Berlin and Chile.

Extraordinary March of Solar Radiation 1919–20.—For about six years the intensity of solar radiation has almost always exceeded the mean value, 1.933 calories per square centimeter per minute, which was found from the Washington, Mt. Wilson and Mt. Whitney observations of 1902–12, as published in Volume III of the Annals of the Astrophysical Observatory. This condition of affairs was expected to attend the return of increased solar activity, otherwise evidenced by numerous sunspots,

DATE	SATURN—α LEONIS	PHASE ANGLE	SATURN ☉ LONGITUDE	EARTH ☉ LONGITUDE	Δ	SOLAR LAG. 25.4 Δ / 360 DAYS	NEAREST CORRESPONDING DATE, CALAMA	SOLAR CONSTANT	GRADE	CORRECTION FOR PHASE* M.	CORRECTED SATURN—α LEONIS. M.
Jan. 29.6	+0.743	3.18°	157° 13′	128° 55′	28° 18′	2.0	Jan. 27	1.975	S	—0.079	+0.664
Feb. 8.6	0.715	2.16	36	139 3	18 33	1.3	Feb. 7	1.946	U+	0.054	0.661
14.5	0.704	1.53	49	140 59	16 50	1.2	13	1.962	U+	0.038	0.666
16.5	0.701	1.30	53	147 5	10 48	0.8	15	1.951	S—	0.032	0.669
17.5	0.690	1.18	55	148 6	9 49	0.7	17	...	...	...	...
18.6	0.687	1.07	58	149 7	8 51	0.6	18	1.971	S—	0.027	0.660
19.5	0.681	0.96	158 0	150 6	7 54	0.6	19	1.983	S—	0.024	0.657
23.5	0.637	0.53	8	154 7	4 1	0.3	23	...	...	...	...
25.5	0.633	0.34	12	156 7	2 5	0.1	25	1.987	E—, S	0.008	0.625
28.5	0.614	0.25	18	159 8	—0 50	—0.1	28	1.953	S—	0.040	0.604
Mar. 1.5	0.653	0.40	22	161 8	—2 45	—0.2	Mar. 1	1.980	S—	0.016	0.637
9.5	0.711	1.26	40	169 8	—10 28	—0.7	10	1.959	S	0.049	0.662
13.5	0.708	1.70	48	173 6	—14 18	—1.0	14	1.962	VG, S	0.066	0.642
24.4	0.783	2.85	159 11	183 58	—24 8	—1.7	26	1.953	S	0.111	0.672
Apr. 25.5	0.784	2.96	13	185 03	—25 8	—1.8	27	1.966	E, S	0.115	0.669
12.4	0.854	4.54	51	202 41	—42 8	—3.0	Apr. 15	1.944	S—	0.177	0.677
23.4	0.860	5.27	160 14	213 26	—53 2	—3.7	26	1.960	VG+, S	0.205	0.655
May 11.4	0.899	6.04	52	230 52	—70 0	—4.9	May 16	1.957	S	0.235	0.664

* 0.025 and 0.039 phase coefficients before and after opposition.

prominences, faculae. We have now, however, long passed the period of maximum sunspots, so that we should naturally expect the sun's radiation to be falling below the mean value of 1902–12. The results obtained by the Smithsonian observers at Calama, Chile, indicate quite otherwise.

I have computed solar radiation values for each five days interval from July 1, 1919 to March 25, 1920. The mean value is never based on less than two observations, and this minimum occurs only in two instances. All other values depend on three days of observation, more often four, and very often five.

One is immediately struck by the wide fluctuation of the mean values shown. The fluctuation of individual days naturally had a still wider range, reaching in fact to 8%. The mean values cover a range of 5%. With gradually diminishing swings, up and down, the radiation fell from June 1919 to early in October, then suddenly leaped up to a high mean value which it maintained until early in December, and then again suddenly leaped much further and remained from the end of December to the middle of March 1920 at a mean value far in excess of anything which we have any record of, continued for so long a time as three months during the whole fifteen years in which solar constant observations have been carried on with anything like regularity. Towards the end of March an extremely rapid fall of radiation occurred, so that individual values have run as low as 1.86 calories.

1919	A	B	C	D	E	F
June	46	84	37	39	71	53
July	36	54	47	63	57	31
Aug.	53	54	38	36	51	45
Sept.	28	33	30	42	31	30
Oct.	18	57	49	46	59	62
Nov.	60	51	60	43	47	54
Dec.	55	48	54	60	67	81
1920						
Jan.	69	102(?)	74	78	81	70
Feb.		87	60	78	77	68
Mar.	77	65	70	50	10	

In view of this extraordinary march of solar radiation values, it may be recalled that we have been passing through an exceptionally cold and cloudy winter from about the first of December. The cloudiness has prevailed in South America as well as here, so that if it had not been for the introduction of the new method of observing, of which notice was given to the Academy at its last meeting, the observers would not have been able to give us this very continuous record.

At first sight it looks paradoxical that a cold winter could accompany

extraordinarily high values of solar radiation, but it has been not only a cold winter but a cloudy winter. Hence it may have been that the direct effect of the outburst of solar activity was to produce excessive cloudiness which by high reflection diminished the radiation available to warm the earth.

In the preceding table I give the mean values of the solar radiation above mentioned. In each month I have indicated the successive five day periods by the capital letters A, B, C, D, E, and F. The values given are the number of thousandths of a calorie by which the solar radiation of a given time interval exceeds 1.900. Thus, for the first period of June the mean value is 1.946.

March Values.—On or about March 22, great sunspot activity was reported. On March 22 and 23 there were intense magnetic disturbances affecting all observations of terrestrial magnetism and the operation of telegraphs and cables. Remarkable auroral displays followed. In connection with these conditions it is interesting to note the very unusual progress of the solar constant of radiation during the month of March. This is given in the following table

Date	Mean,	11 to 17	18	19	20	21	22	23	24
Value		1.968	1.954	1.940	1.931	1.941	1.927	1.866	1.905

It is highly probable that the results just given will have a special significance in connection with the remarkable outbreak of solar activity to which attention has been drawn.

THE PERMANENT GRAVITATIONAL FIELD IN THE EINSTEIN THEORY

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Communicated by E. H. Moore, June 7, 1920

1. In accordance with the theory of Einstein a permanent gravitational field is defined by a quadratic differential form

$$ds^2 = \sum_{i,k}^{1,\ldots 4} g_{ik}dx_i dx_k, \quad (g_{ik} = g_{ki}), \tag{1}$$

where the g's, called the potentials of the field, are determined by the condition of satisfying ten partial differential equations of the second order, $G_{ik} = 0$. When the four coördinates x_i are functions of a single parameter, the locus of the point with these coördinates is a curve in four-space. If these functions are of such a character that the integral

$$\int \sqrt{\Sigma g_{ik}dx_i dx_k} \tag{2}$$

is stationary along the curve, the curve is called a "world-line," or a geodesic, in the four-space.

Einstein[1] considered the case when x_1, x_2, x_3, are rectangular coördinates and x_4 represents the time, and assumed that the field was produced by a mass at the origin which did not vary with the time. In order to obtain the equations of the world-lines in the form which enabled him to establish his well-known expression for the precession of the perihelion of Mercury, Einstein made also the following assumptions:

A. The quantities g_{ik} are independent of t.

B. The equations $g_{i4} = 0$ for $i = 1, 2, 3$.

C. The solution is spacially symmetric with respect to the origin of coördinates in the sense that the solution is unaltered by an orthogonal transformation of x_1, x_2, x_3.

D. The quantities $g_{ik} = 0$ for $i \neq k$ at infinity and also $g_{44} = -g_{11} = -g_{22} = -g_{33} = 1$. Schwarzschild,[2] using the first three of these assumptions and certain others integrated the equations $G_{ik} = 0$, and obtained (1) in the form

$$ds^2 = \left(1 - \frac{\alpha}{R}\right) dt^2 - \frac{dR^2}{1 - \frac{\alpha}{R}} - R^2(d\theta^2 + \sin^2\theta d\varphi^2), \qquad (3)$$

where α is a constant depending on the mass at the origin. Levi-Civita[3] has given three solutions of the equations $G_{ik} = 0$, one of which includes the above, and Weyl[4] has given still another solution. Later, Kottler[5] obtained the form (3) not by the solution of the equations $G_{ik} = 0$ but as a consequence of certain postulates. It is the purpose of this paper to accomplish the same result by the following set of postulates:

I. Assumptions A and B of Einstein, in accordance with which we write (1) in the form

$$ds^2 = V^2dt^2 - ds_0^2, \qquad (4)$$

where

$$ds_0^2 = \sum_{ik}^{1,2,3} a_{ik}dx_i dx_k, \qquad (5)$$

the functions V and a_{ik} being independent of t.

II. The function V is a solution of

$$\Delta_2 V = 0, \qquad (6)$$

where $\Delta_2\theta$ is the Beltrami differential parameter formed with respect to the form (5), and is defined by

$$\Delta_2\theta = \frac{1}{\sqrt{a}} \sum_{i,k}^{1,2,3} \frac{\partial}{\partial x_i} \left(\sum_{k}^{1,2,3} a^{(ik)} \sqrt{a} \frac{\partial\theta}{\partial x_k} \right), \qquad (7)$$

where a is the determinant of the functions a_{ik} and $a^{(ik)}$ is the co-factor

of a in this determinant divided by a. This assumption is equivalent to the equation $G_{44} = 0$.

III. The surfaces V = const. form part of a triply orthogonal system in the space, S_3, of coördinates x_1, x_2, x_3.

IV. The orthogonal trajectories of V = const. in S_3 are paths of the particle, in the sense that the coördinates x_1, x_2, x_3, of a world-line determine a path in S_3 of a particle in the gravitational field for which the world-line is the representation in terms of space and time t.

V. The form (5) is euclidean to a first approximation.

2. In order to simplify the equations, we take (5) in the form

$$ds_0^2 = \sum_i^{1,2,3} a_i dx_i^2. \tag{8}$$

If we choose s for the parameter along a world-line and apply the Euler equations of condition that the integral

$$\int \sqrt{V^2 dt^2 - ds_0^2}$$

be stationary along the line, we get

$$\frac{d^2x_i}{ds^2} + \sum_j \frac{\partial \log a_i}{\partial x_j} \frac{dx_i}{ds} \frac{dx_j}{ds} - \frac{1}{2a_i} \sum_j \frac{\partial a_j}{\partial x_i} \left(\frac{dx_j}{ds}\right)^2 + \frac{V}{a_i} \frac{\partial V}{\partial x_i} \left(\frac{dt}{ds}\right)^2 = 0, \tag{9}$$

$$\frac{dt}{ds} = \frac{k}{V^2}, \tag{10}$$

where k is a constant. In these equations and hereafter the symbol $\sum_j$ means the sum for $j = 1, 2, 3$.

We inquire under what conditions the path of a particle in S_3 is a geodesic, that is a curve along which the integral $\int \sum_i a_i dx_i^2$ is stationary. When s_0 is taken for the parameter along such a geodesic, we find that

$$\frac{d^2x_i}{ds_0^2} + \sum_j \frac{\partial \log a_i}{\partial x_j} \frac{dx_i}{ds_0} \frac{dx_j}{ds_0} - \frac{1}{2a_i} \sum_j \frac{\partial a_j}{\partial x_i} \left(\frac{dx_j}{ds_0}\right)^2 = 0. \tag{11}$$

From (4) and (10) it follows that the parameters s and s_0 along a world-line and the corresponding path in S_3 are in the relation

$$ds_0 = \sqrt{\frac{k^2}{V^2} - 1}\, ds. \tag{12}$$

With the aid of this relation we find that in order that equations (9) and (11) define the same curves in S_3, we must have

$$\frac{dV}{ds_0} \frac{dx_i}{ds_0} - \frac{1}{a_i} \frac{\partial V}{\partial x_i} = 0 \quad (i = 1, 2, 3). \tag{13}$$

These are the conditions that the path be an orthogonal trajectory of the surfaces V = const. When we require that equations (11) and (13)

be consistent, we find that it is necessary and sufficient that ΔV be a function of V, say

$$\Delta V = \varphi(V), \tag{14}$$

where ΔV is the first differential parameter of V with respect to the form ds^2_0. For the form (5) its expression is

$$\Delta V = \sum_{ik} a^{(ik)} \frac{\partial V}{\partial x_i} \frac{\partial V}{\partial x_k}. \tag{15}$$

When (14) is satisfied by a function V, the surfaces V = const. are said to be *geodesically parallel.* Hence we have the theorem:

A necessary and sufficient condition that a path in a gravitational field be a geodesic in S_3 is that it be one of the orthogonal trajectories of the surfaces V = const., which must form a geodesically parallel family.

3. The function V is interpreted as the velocity of light in the field, and consequently along a world-line of a ray of light $ds = 0$, as follows from (4). In order to find the equations of these world-lines we apply the Fermat principle that $\int dt$ be stationary along such a line, that is the integral $\int \sqrt{\frac{1}{V^2} \Sigma a_i dx_i^2}$. This gives the equations

$$\frac{d^2x_i}{dt^2} + \frac{dx_i}{dt} \sum_j \frac{\partial}{\partial x_j} \log \frac{a_i}{V^2} \frac{dx_j}{dt} - \frac{V^2}{2a_i} \sum_j \frac{\partial}{\partial x_i} \left(\frac{a_j}{V^2}\right) \left(\frac{dx_j}{dt}\right)^2 = 0.$$

When we require that the path of a ray of light be a geodesic in S_3, we obtain equations (13) and (14) as formerly. Hence:

When the orthogonal trajectories of the surfaces V = const. are paths of a particle in a gravitational field, they are also the paths of a ray of light; and conversely.

4. In accordance with III we choose the coördinates x_1, x_2, x_3, so that V is a function of x_1 alone and we have (8). Then from IV, which is equivalent to (14), written $\Delta V = \varphi(x_1)$, and II we have

$$a_1 = \frac{(V')^2}{\varphi}, \quad a_2 a_3 = \frac{\psi^2}{\varphi}, \tag{16}$$

where the prime indicates differentiation with respect to x_1 and ψ is independent of x_1.

If $d\bar{s}_0^2 = \Sigma \bar{a}_i dx_i^2$ is the linear element of euclidean space, the functions $\bar{a}_i$ must satisfy the six equations of Lamé.[6] If a_1 is to be a function of x_1 alone and the second of (16) is to be satisfied, it can be shown that the coördinates x_1 can be chosen, so that

$$d\bar{s}_0^2 = dx_1^2 + x_1^2(\sigma^2 dx_2^2 + \tau^2 dx_3^2), \tag{17}$$

where σ and τ are independent of x_1 and satisfy

$$\frac{\partial}{\partial x_2}\left(\frac{1}{\sigma}\frac{\partial \tau}{\partial x_2}\right) + \frac{\partial}{\partial x_3}\left(\frac{1}{\tau}\frac{\partial \sigma}{\partial x_3}\right) + \sigma\tau = 0. \tag{18}$$

This is the condition that the expression in parenthesis in (17) is the linear element of the unit sphere.[7]

If we write

$$V^2 = c^2(1 + 2\varphi_1(x_1))$$

where c is the constant velocity of light, and in accordance with assumption V require that (16) be satisfied by expressions approximating the coefficients in (17), we obtain $\varphi_1 = -\frac{b}{2cx_1}, \frac{1}{a_1} = 1 + 2\varphi_1$, where b is a constant. Hence, if we take $\sigma = 1, \tau = \sin x_2$, which is a set of solutions of (18), we obtain the form (3). Another choice gives at once one of the forms found by Levi-Civita.[3]

[1] *Berlin Sitzungsberichte*, 1915 (831).
[2] *Ibid.*, 1916 (189).
[3] *Rendiconti dei Lincei* (Ser. 5), **27**, 1918 (350).
[4] *Ann. Physik*, **54**, 1917 (117).
[5] *Ibid.*, **56**, 1918 (401).
[6] Eisenhart's *Differential Geometry*, (449).
[7] *Ibid.*, (157).

A SIMPLIFIED METHOD FOR THE STATISTICAL INTERPRETATION OF EXPERIMENTAL DATA

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One of the fundamental postulates of the law of probability of errors is that positive and negative errors are equally frequent and that, therefore, the arithmetical mean is the most probable mean. This is true when we are dealing with *small independent errors*, but in cases of *interdependent* values of natural *frequencies* (physical, biological, agricultural), it may or may not be true, depending upon the maximum deviation from the mean. Thus we can conceive of a molecule of oxygen gas with a momentary velocity of zero or of "infinity."[1] Yet the average velocity as determined from density and pressure measurements is but a few hundred yards per second, a value not very far from zero, but infinitely different from "infinity." When the frequencies of such data are plotted on rectangular coördinate paper, we obtain what are called skew curves. Within the last twenty-five years a great deal has been written concerning skew curves and their types, and, judging from the number which have thus far appeared in print, they promise to be of infinite variety. To these various types of frequency curves have been fitted mathematical formulas and with their aid statistical constants have been obtained, many of which we have reason to believe are theoretically inapplicable and practically misleading.

In a paper now in press and another in preparation, it is shown that all the types of frequency curves thus far published, excepting those having a zero class, conform to one mathematical expression. It is pointed out also that it is futile to try to fit discontinuous irregular frequencies as well as those having a zero class to mathematical formulas, since the statistical constants obtained from such formulas are too often misleading. For these types of natural or perhaps unnatural frequencies a graphical method is developed capable of yielding any desired degree of accuracy; that is, within experimental error. The general equation referred to above is,

$$\frac{y}{y_0} = e^{-k^2\left(\log \frac{m}{m_0}\right)^2} \qquad (1)$$

where m denotes the numerical value of any measurement, m_0 the value of the mean, e the base of natural logarithms, y any frequency, and y_0 a frequency of the probability of a deviation zero.

Obviously, when in equation (1), m is greater than zero and less than twice m_0, we may express the exponent of e in series, thus,

$$\frac{y}{y_0} = e^{-k^2\left[\left(\frac{m}{m_0}-1\right)-\frac{1}{2}\left(\frac{m}{m_0}-1\right)^2+1/3\left(\frac{m}{m_0}-1\right)^3\cdots\right]^2}. \qquad (2)$$

Neglecting all terms but the first, we obtain,

$$\frac{y}{y_0} = e^{-k^2\left(\frac{m-m_0}{m_0}\right)^2} = e^{-h^2(m-m_0)^2} = e^{-h^2x^2}, \qquad (3)$$

which is identical with the usual form of the equation for the probability of errors, and which is but an approximation of equation (1).

In order to minimize the labor and time required to perform a large set of calculations, often running into the thousands, equation (3) was transformed into a rectilinear one, thus,

$$\text{Log (Log } y_0/y) = 2 \text{ Log } x + 2 \text{ Log } h - 0.3623 = 2 \text{ Log } x + K \qquad (4)$$

With a few determinative values for x read off on the frequency polygon constructed from the experimental data, we may obtain the value for K, which is the distance on the Log (Log y_0/y) axis from the origin to the point of intersection. We can then calculate the several statistical constants from the value of K; for example, the index of precision, h; the probable error, x; the probable error of the mean, x_0; the standard deviation; the coefficient of variability, etc.; or,

$$h = (10)^{\frac{k+0.3623}{2}},$$

$$x = 0.4769\,(10)^{-\frac{k+0.3623}{2}},$$

$$x_0 = \frac{x}{\sqrt{n}} = \frac{0.4769}{\sqrt{n}}(10)^{-\frac{k+0.3623}{2}}, \text{ etc.}$$

Details of the method, as well as numerous examples from biology, genetics, physics and agriculture will be given in two subsequent papers.

[1] Actually it was found that the chances are 20000 : 1 that a molecule of oxygen gas would have a resultant velocity, at 0° C., of less than 50 meters per second, or greater than 2500 meters per second, the mean being 353.6 meters per second. Here the mean is not the arithmetical mean of the variables, but the nth root of the products of the n (dependent) variables. The theoretical basis for this will be given in another paper. For a mathematical discussion see Galton and McAlister, *Proc. Roy. Soc. Lond.*, **29**, 1879 (365).

A CRITICAL STUDY OF FERTILIZER EXPERIMENTS

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Among the most expensive and time-consuming experiments in agricultural investigations have been those which attempt to ascertain the proper chemical amendments or fertilizers for soils. This applies in particular to the long-term fertilizer experiments like those at Rothamsted in England, at State College in Pennsylvania, and at Wooster and Strongsville in Ohio. Conceived and inaugurated, as they were, at times when little or no real authentic information was available relative to the nature of soils and plants, it is but natural that fallacious and short-sighted planning should have dominated them. It occurred to one of us that as critical thinking in this field has become more general, and facts more plentiful, it is high time that fertilizer experiments in general and the "long-term" experiments in particular be subjected to critical scrutiny. It seemed desirable to employ the statistical method for this purpose, particularly in view of the striking results obtained in this laboratory by our former associate, D. D. Waynick. It seemed clear to one of us that if, as Waynick, and Waynick and Sharp had demonstrated, the variability of soils and of plants is very large even within selected and presumably uniform material, one could not expect previous fertilizer experiments to be of much value, since the factor of variability has been entirely ignored in their arrangement and study, and the probable error to which they were subject was not determined. Accordingly, Lipman and Waynick began in January, 1919, a systematic study by statistical methods of the results of fertilizer experiments at the Ohio and at the Pennsylvania Agricultural Experiment Stations. Mr. Waynick left this laboratory the following July, but with a number of interruptions, the work has been continued, and we hope to issue the voluminous data, together with a critical discussion of them, in due course. Since the work may be a long time in the press, we deem it wise to present here a few of the salient and most im-

portant findings of our studies, so that our colleagues may be apprised of what we consider to be an investigation of a fundamental nature, not merely on account of the importance of the subject itself, but because of its important bearings on agricultural research.

It seems that the originators of both the Ohio and the Pennsylvania experiments saw the value of replicating check plots, while not recognizing the value of such replication for the treated plots. Only in the case of two complete fertilizer plots in the Ohio experiments, was the fertilizer treatment the same. In all the others every treatment was different from that of every other. This situation renders it difficult to subject their data to statistical treatment in the most desirable way. Fortunately, however, the long series of years during which the plots were studied gives, in a certain sense, a replication of plots of each kind. Our procedure has been, therefore, to group the plots in different ways including the following:

1. All the check plots for each year.
2. One check plot for all the years.
3. All the plots treated with "one-element" fertilizers in one year.
4. Every "one-element" fertilizer plot for all the years.
5. The same double study for the "two-element fertilizer plots."
6. The same for the "three-element" fertilizer plots.

In addition to these groupings, others were made in which a given plot was studied with each crop in the rotation, so as to allow of only three to eight "yield" data for each plot. It may be said in passing that the rotation study included in these experiments only serves to complicate a situation which was already sufficiently difficult. We shall show in detail in the complete study which is to be published, that these experiments are utterly inadequate for solution of the questions involved and that all such fertilizer experiments are so fallacious as that they do not justify the use of the large amounts of money that are constantly being lavished upon them.

For the sake of brevity, only a few of our findings, from the study of the Ohio data alone, are summarized here.

1. The "one-element" fertilizer treatments show no significant increases in yield over the yields obtained on the untreated check plots. All statements to the contrary which have heretofore been made are erroneous and the data on which they are based were obtained by a misleading method of procedure and evaluation.

2. The "two-element" fertilizer plots give definite increases in yield over the untreated control plots. Whether or not the increases are profit-yielding, however, is a question which will be discussed later.

3. The "three-element" fertilizer plots give definite increases in yield over both the untreated control plots and the "two-element" fertilizer plots. Here again the question whether the increases are profit-yielding still remains to be determined.

4. The kind of fertilizer used seems to have been without significance, one being just as good as another, subject to the limitations above noted.

5. The amount of fertilizer used seems likewise to have been without significance (subject to the same limitations).

6. Even when fertilizer experiments are properly planned and the results adequately studied by statistical methods, our present knowledge of the enormous variability of all soils and plants renders the data from any given fertilizer plot of value only on that plot, no matter how near the experimental one. This important consideration renders it highly probable that no fertilizer experiment as ordinarily conducted is possessed of sufficient practical value to justify the large expenditure of money, time, and energy involved.

We wish to emphasize that we are not desirous of making a fetish of the application of statistical study to fertilizer experiments. Nevertheless, we must say that if statistical methods, inadequate as they may be, should not prove applicable to an evaluation of the results of fertilizer experiments, the latter must be accounted of even less value and significance than we have here accorded to them.